THE

AMERICAN NATURALIST

VOL. XLVI | May, 1912 | NO. 545

THE CONTINUOUS ORIGIN OF CERTAIN UNIT CHARACTERS AS OBSERVED BY A PALEONTOLOGIST[1]

DR. HENRY FAIRFIELD OSBORN

RESEARCH PROFESSOR OF ZOOLOGY, COLUMBIA UNIVERSITY, CURATOR EMERITUS OF VERTEBRATE PALEONTOLOGY IN THE AMERICAN MUSEUM OF NATURAL HISTORY, VERTEBRATE PALEONTOLOGIST UNITED STATES GEOLOGICAL SURVEY

II. EVIDENCES FOR CONTINUITY

Abandoning the historical background, we come to our own subject, *the origin and establishment in continuity of characters which when established exhibit many of the distinctive features of unit characters, namely, segregation, stability, pure heredity, and possibly, although this has not yet been demonstrated, dominance and recession in successive generations.*

In fifteen previous papers of the writer beginning in 1889[25] the observation is repeatedly made that all absolutely new characters which we have traced to their very beginnings in fossil mammals arise gradually and continuously. One by one these characters, which are independently changing in many parts of the organism, at the same time accumulate until they build up a degree of change which paleontologists designate as a "mutation"

[25] Osborn, H. F., "The Paleontological Evidence for the Transmission of Acquired Characters," AMER. NATURALIST, Vol. XXIII, No. 271, July, 1899, pp. 561–566.

in the sense of Waagen, who proposed this inter-specific term in 1869. Finally they reach a sufficiently important phase to designate the stage as a species.[26]

These new characters were first (1891) termed "definite variations"; subsequently (1907)[27] the term "rectigradations" was applied to them. Rectigradation is merely a designation for the earliest discernible stages of certain absolutely new characters. It involves no opinion nor hypothesis as to genesis; it is a simple matter of observation. Referring to the figure (p. 274) of the upper grinding teeth of the horse, the majority of the fourteen characters have been observed to arise as rectigradations.

Quite different is the allometron. This is a new designation for the continuous change of proportion in an existing character which may be expressed in differences of measurement. Since 1902 and especially during the past year the behavior of allometrons has been very carefully investigated by myself and by my colleague, Dr. W. K. Gregory.

RECTIGRADATION = a qualitative change, the genesis of a new character.

ALLOMETRON = a quantitative change, the genesis of new proportions in an existing character.

The distinction between a rectigradation and an allometron is readily grasped: when the shadowy rudiment of a cusp or of a horn first appears it is a rectigradation; when it takes on a rounded, oval or flattened form this

[26] This sentence may be contrasted with that of Punnett (*op. cit.*, p. 15): "Speaking generally, species do not grade gradually from one to the other, but the differences between them are sharp and specific. Whence comes this prevalence of discontinuity if the process by which they have arisen is one of accumulation of minute and almost imperceptible differences? Why are not intermediates of all sorts more abundantly produced in nature than is actually known to be the case?"

[27] Osborn, H. F., "Evolution of Mammalian Molar Teeth to and from the Triangular Type," 8vo, Macmillan Company, September, 1907.

change is an allometron. In mammals rectigradations are comparatively few; allometrons comprise the vast number of changes in the hard parts. In the origin of cusp and horn rudiments rectigradations are parallel (see Fig. 3), in the changing proportions of a skull allometrons are divergent (Figs. 1, 3).

Granting, without at present considering the evidence,[28] that these rectigradations and allometrons arise continuously through entirely unknown laws, that they are blastic or germinal characters, the question arises, do they become separable as unit or alternating characters in heredity.

In general, paleontology furnishes quite as strong proof as Mendelism or experimental zoology *as to the individuality, separableness, and integrity of single characters in evolution.* But, whether both rectigradations and allometrons are separable in heredity can only be demonstrated through experiments on cross breeding or hybridizing.

The special object of this Harvey lecture is to show that certain at least of the rectigradations and allometrons observed in mammals are separable in heredity, that they split up into larger and smaller groups or units, some into partially blending units, others into absolutely distinct or non-blending unit; finally that at least in the first cross they exhibit dominance.

The very important remaining question whether, like the quality of "tallness" or "shortness" in Mendel's classic experiments on the pea, these allometrons continue to split into dominants and recessives in later crosses, has not been investigated but is probably capable of investigation in mammals which do not become sterile in the first hybrid generation.

Five examples of the continuous evolution of rectigradations and allometrons may be cited, namely:

[28] This evidence is for the first time fully presented in the writer's monograph on the "Titanotheres," in preparation for the U. S. Geological Survey.

1. Skull and horns of titanotheres (Figs. 1, 3, 4).
2. The horns of cattle (Fig. 2).
3. The cranium of man (Fig. 1).
4. The skull of horses (Figs. 4, 5, 6, 7).
5. Teeth (Fig. 8).

One of the most salient examples of the genesis of unit characters through continuity is that of the evolution of horns, *i. e.*, of the osseous prominences on the skull. Horns are now known definitely to be "unit characters," first through their sudden and complete disappearance in the niata and polled breeds of cattle; second, because they conform to the laws of sex-limited inheritance. The question is, do horns originate continuously or discontinuously?

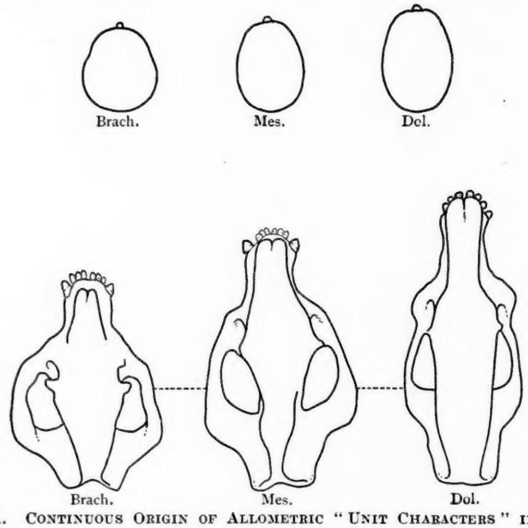

FIG. 1. CONTINUOUS ORIGIN OF ALLOMETRIC "UNIT CHARACTERS" IN THE CRANIUM (*A*) AND SKULL (*B*) OF MAN AND TITANOTHERES.

A, Man	Brachycephaly	Mesaticephaly	Dolichocephaly
B, Titanotheres	Brachycephaly (*Palæosyops*)	Mesaticephaly (*Manteoceras*)	Dolichocephaly (*Dolichorhinus*)

1. *Horns of Titanotheres*

The titanotheres are an extinct family of quadrupeds distantly related to the horses, tapirs and rhinoceroses,

to the evolution of which the author has devoted twelve years of investigation, assisted by Dr. W. K. Gregory. As set forth in an earlier contribution[29] the genesis of horns as rectigradations has been observed in four or five distinct phyla of titanotheres. These phyla descend independently from a single ancestor of remote geologic age. Both in respect to new cusps on the teeth and new horn rudiments on the skull there is observed what in our ignorance may be called an ancestral predisposition to the genesis of similar rectigradations. This predisposition betrays the existence of *law* in the origin of certain new characters; it recalls a sagacious remark of Darwin:

> . . . The principle formerly alluded to under the term of *analogical variation* has probably in these cases often come into play; that is, the members of the same class, although only distantly allied, have inherited so much in common in their constitution, that they are apt to vary under similar exciting causes in a similar manner; and this would obviously aid in the acquirement through natural selection of parts or organs, strikingly like each other, independently of their direct inheritance from a common progenitor.[30]

Briefly, the origin of the titanothere horns is as follows: (*a*) from excessively rudimentary beginnings, *i. e.*, rectigradations, which can hardly be detected on the surface of the skull; (*b*) there is some predetermined law or similarity of potential which governs their first existence, because (*c*) the rudiments arise independently on the same part of the skull in different phyla at different periods of geologic time; (*d*) the horn rudiments evolve continuously, and they gradually change in form (*i. e.*, allometrons); (*e*) they finally become the dominant characters of the skull, showing marked variations of form in the two sexes; (*f*) they first arise in late or adult stages of growth, but are pushed forward gradually into

[29] "The Four Inseparable Factors of Evolution. Theory of their Distinct and Combined Action in the Transformation of the Titanotheres, an Extinct Family of Hoofed Animals in the Order Perissodactyla," *Science*, N. S., Vol. XXVII, No. 682, January 24, 1908, pp. 148–150.

[30] "Origin of Species," Vol. II, p. 221.

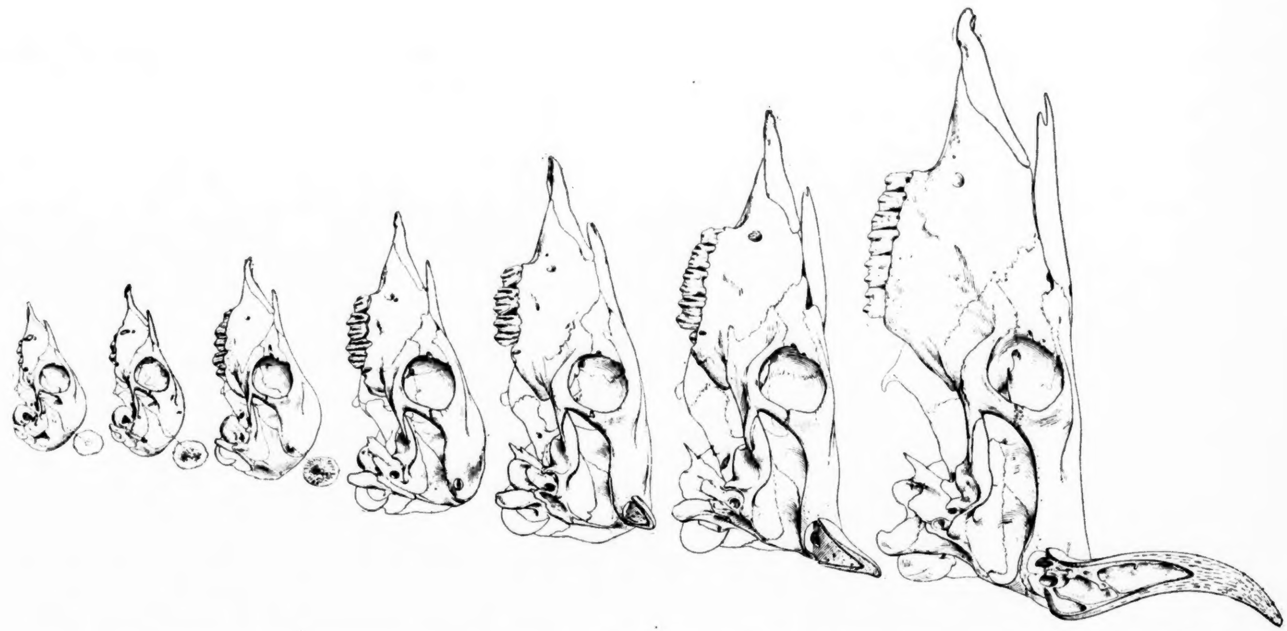

FIG. 2. CONTINUITY IN THE ONTOGENESIS OF THE HORN AND HORN SHEATH IN CATTLE IN SEVEN STAGES, 1–7. After preparations by Mr. S. H. Chubb in the collections of the American Museum of Natural History.

1. Adult, 9 years, completed osseous horn and horny sheath. 2. Yearling, 18 months, continuous shifting of osseous horn to occiput. 3. Calf, 2 months, continuous shifting of osseous horn to occiput. 4. Calf, 2 weeks, continuous shifting of osseous horn to occiput. 5. Fœtal stage, 9th month, bony swelling, and epidermal swelling pointed. 6. Fœtal stage ?6–7th month, epidermal swelling, covered with pointed hair tuft. 7. Fœtal stage, ?5th month, epidermal swelling, covered with 40 scattered hairs.

earlier and earlier ontogenic stages until they appear to arise prenatally.

In the titanotheres (Fig. 3) the bony swelling is seen at the junction of the nasals and frontals (black shading), in dolichocephalic skulls it appears chiefly on the nasals, in brachycephalic skulls chiefly on the frontals. Its original low, rounded shape is like that seen in the ontogeny of the horns in cattle.

2. *Horns of Cattle*

The phylogenesis of the horns in titanotheres (Fig. 3) is exactly similar to the ontogenesis of the horns in Bovidae (Fig. 2), in which the dermal rudiments first appear soon after the complete formation of the bones of the skull in the unborn young, and the osseous rudiments appear as rounded protuberances in the 8th month.

In the ontogenesis of horns in cattle three distinct elements are involved: (*a*) a psychic predisposition to use the horn, (*b*) a dermal thickening over the bony horn swelling which in ontogeny precedes the swelling, (*c*) appearance of the bony swelling itself.

The ontogenesis is observed to be accompanied by a marked allometric change in the skull which shifts the horn backward from the side of the cranium to the side of the occiput by the obliteration of the parietal bones.

3. *Cranium of Man.*

A third instance of continuous development is that of the form of the cranium in man (Fig. 1), an allometric evolution, or change of proportion, which is of especial significance because, according to the unanimous testimony of anthropologists,[31] head form is the result of very gradual change either in the elongate (dolichocephalic) or broadened (brachycephalic) direction.

[31] Ripley, Wm. Z., "The Races of Europe, a Sociological Study," 8vo, D. Appleton & Co., 1899, 624 pp.

The matter is directly pertinent to the present discussion because "long heads" and "broad heads" are continuously crossing and we know what the direct and ultimate effects of such crosses are. The evidence has important bearing also on the influence of selection, environment, and inheritance or the effects of use and disuse.

Determination of the proportions of the cranium or the cephalic index is one of the standard tests or race; it is an expression of the greatest breadth of the head above the ears and the percentage of its greatest length from the forehead (glabella) to back, the latter measurement being taken as 100. Three types adopted by anthropologists are:

	Extreme Range
Brachycephalic, 80.1 and above	100–80
Mesocephalic, 75.1–80	80–75
Dolichocephalic, 75 and below	75–62

Among the present races of Europe the widest limits of variation between brachycephaly and dolichocephaly are in the averages between 73 and 87; individual extremes of 62 and 100 have, however, been observed. These extremes in European head form do not coincide either with geographic or political boundaries, but are attributed to the entrance into Europe of brachycephalic and dolichocephalic types which evolved in Asia. Similarly among the aborigines in America the indices range from a low dolichocephaly as among the Delaware, Pima Indians, etc., to a decided brachycephaly as among the Athabascan tribes in Panama, Peru, and other localities. A significant fact in Europe is that dolichocephaly and brachycephaly are extremely stable characteristics in heredity. The significant fact in America is that through a very long period of time the various races of Indians, who are believed to have had originally a similar origin, have acquired under conditions of geographic isolation considerable diversity in the proportions of the head. Similarly A. Keith[32] from the present distribution of the

[32] Keith, A., *Journ. Royal Anthropological Institute,* 1911. See *Nature,* Vol. 88, No. 2195, November 23, 1911, p. 119.

Negro tribes in equatorial Africa has reached the following conclusions:

> There has been free intermigration; in the course of their evolution, the tendency of one tribe has been towards the accentuation of one set of characters, of another towards another set. Thus the Dinka acquire high stature and narrow heads; the typical Nigerians low stature and narrow heads; the Basoko wide, short heads and low stature; the Buruns wide heads and high stature. Interbreeding may have played its part; but if it had played a great part we should have found greater physical uniformity than there is. The influence of Arab blood on these tribes has probably been exaggerated.

It appears that environment has not any direct influence on head form, but that geographical isolation affords the several varieties of man as well as other mammals a chance to develop their peculiar head characters. Elliot Smith states (letter, August 12, 1911):

> In my opinion the conditions of dolichocephaly and brachycephaly must have developed very slowly through exceedingly long periods of time and in widely separated areas amidst widely different environments. Brachycephaly is especially distinctive of the Central Asian high plateau populations, dolichocephaly of the littoral and plain-dwelling peoples; but these "unit characters" are now so fixed that environment is powerless to modify them in a thousand years or so. . . . I do not believe for a moment in Boas [that is, in Boas's observations (1911) on the rapid influence of environment in modifying head form].

Elliot Smith takes very strong ground as to the lack of evidence that environment directly produces any modification of head form; he implies that such modification, if natural, would only show itself after thousands of years of residence; environment no doubt has indirect influence. Hrdlička, on the other hand, has obtained definite results in the influence of environment on the vault and face form of the Eskimo;[33] it remains to be shown how far these changes are ontogenic. The recent conclusions of Boas (1911)[34] that dolichocephaly and brachy-

[33] Hrdlička, Ales, "Contribution to the Anthopology of Central and Smith Sound Eskimo," Anthr. Paper Am. M. N. H., V, Pt. II, 1910, p. 214.

[34] Boas, Franz, "The Mind of Primitive Man," 8vo, Macmillan Company, New York, 1911, 924 pp.

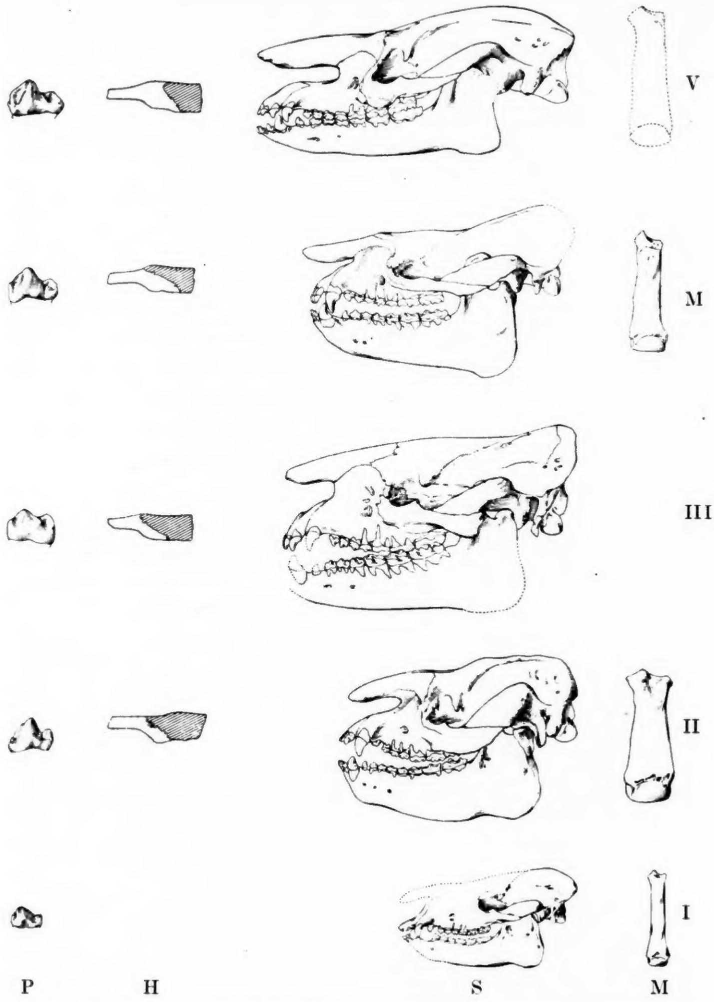

FIG. 3. RECTIGRADATIONS AND ALLOMETRONS IN TITANOTHERES. Continuity in the phylogenesis of osseous horns in titanotheres. P = 2d lower premolar; H = section of nasals and frontals (shaded) showing osseous horn; S = skulls; M = median metacarpal bones.

V. ***Dolichorhinus***, a long-headed (dolichocephalic) titanothere.
IV. ***Manteoceras***, a medium-headed (mesaticephalic) titanothere.
III. ***Telmatherium***, a medium-headed (mesaticephalic) titanothere.
II. ***Palæosyops***, a broad-headed (brachycephalic) titanothere.
I. ***Eotitanops***, an ancestral (mesaticephalic) titanothere.

II–V belong to four independent phyla which diverge in their allometric evolution of head (S) and foot proportion (M) but give rise to independent similar rectigradations in the origin of cusps on the premolar teeth (P) and of osseous horn rudiments (H) on the skull.

cephaly are congenitally altered by environment in the first generation are modified by his statement that this action in bringing diverse head forms together would not go so far as to establish a uniform general type.

No anthropologist has offered any satisfactory explanation as to the adaptive significance of dolichocephaly or brachycephaly. It is well known that these differences of head form are not associated with intellectual ability or mental aptitude. Boas writes (April 8, 1911):

> So far the matter is very perplexing to me. I feel, however, very strongly with you that changes in type are very liable to be progressive in definite directions. . . . To my mind it seems no more difficult to assume that this predetermined direction should continue from generation to generation than to make the much more difficult assumption that notwithstanding all internal changes the egg-cell of one generation should be absolutely identical with that of the preceding generation.

Apart from the disputed question of the direct influence of environment and of human selection there is absolute unanimity of evidence and of opinion on the one point essential to the present discussion, namely, *as to the continuity of allometric variation which establishes different extremes of head form under conditions of geographic isolation.*

Granted that these extremes evolve continuously, do they become discontinuous in heredity?

One of the general results of crossing long-headed and narrow-faced types with broad-headed and broad-faced types is what is known as disharmonic heredity, namely, that condition in which the face and cranium do not hold together, but broad faces may couple with long skulls, or *vice versa* (Boas, 1903).[35] Boas concludes that there can be no question that the mixture of a long-headed and of a short-headed race may lead to disharmonism, one race contributing head form, the other facial expression.

As to stability or segregation in heredity the latest

[35] Boas, Franz, "Heredity in Head Form," *Amer. Anthropologist*, Vol. 5, No. 3, July–September, 1903, pp. 530–538.

opinions of Boas, Elliot Smith and Hrdlicka have been sought. Boas is one of the most positive as to the hereditary stability of head form. He observes (1911, pp. 7-9):

> Among European peoples head proportions are considered among the most stable and permanent of all characteristics. In intermarriage of "dolichocephalic" and "brachycephalic" individuals the children do not form a blend between their parents but inherit either the dolichocephalic or brachycephalic head form. Head form thus constitutes a case of almost typical alternating heredity (p. 55). No evidence has been obtained, however, to show that either brachycephaly or dolichocephaly is dominant. Children exhibit one head form or the other, and the cephalic index or ratio of breadth to length undergoes only slight alteration during growth, or ontogeny.

Elliot Smith (letter of August 12, 1911) is "firmly convinced that the form of cranium, orbits, nose, jaws, limb bones, etc., in the 'Armenoid' and 'Proto-Egyptian' series are very stable or even fixed 'unit characters' which do not really blend, but that certain elements of mosaic assemblage of characters may be grafted on to others belonging to the other race."

Opinions as to Blending.—It will be noted that Boas (1895) admits a certain blending of head form in crosses. Hrdlička (letter, November 1, 1911) speaks even more guardedly as to the hereditary stability of head form. He says:

> As to the head form constituting a "unit character" which does not blend in intermixture, I am not able to give a conclusive opinion, but my experience and other considerations lead me to be very skeptical that such is the case to any great extent. The subject is a very complex one and requires considerable direct investigation in different localities and with different peoples before the exact truth can be known. . . . As to the statement that long or broad head form is a stable or unit character not blending in intermixture, I think that only the first part of the proposition may be held as fairly settled. But even then I should change the word "stable" to "persistent," and qualify the phrase by adding "under no greatly differing and lasting environmental conditions."

That prolonged interbreeding or intermixture tends to break down the stability of hereditary head form is

indicated by Boas, Elliot Smith, and Ripley, as well as by Hrdlička, as quoted above. Thus Ripley (1899), p. 55) observes:

> The plotting of cephalic indices on a map of Europe shows that there is a uniform gradation of head form from several specific centers of distribution outward.

In Italy over 300,000 individuals taken from every little hamlet have been measured. In the extreme south we find the dolichocephalic head form of the typical Mediterranean race; the type changes gradually as we go north until in Piedmont we find an extreme of brachy-

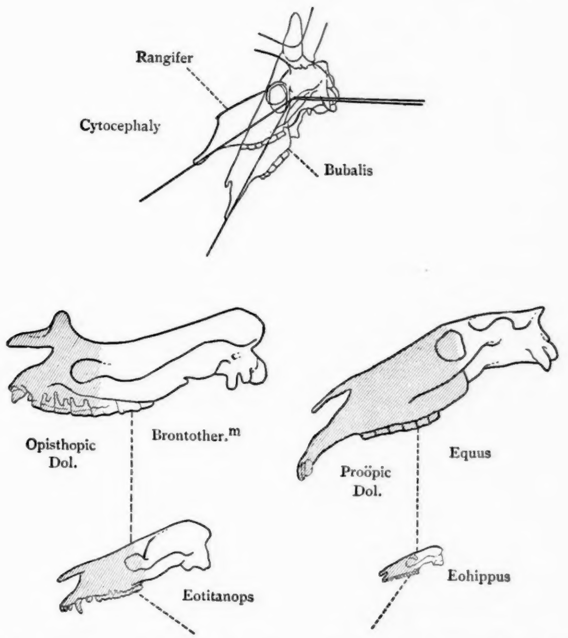

FIG. 4. CONTINUOUS ORIGIN OF ALLOMETRIC "UNIT CHARACTERS" IN THE SKULL OF VARIOUS UNGULATES.

C Cytocephaly,	*Bubalis*	*Rangifer.*
D Dolichocephaly,	Opisthopic	Proöpic.
	(Titanotheres)	(Equines).

In the ancestral *Eotitanops* and *Eohippus* the facio-cranial index is very similar. In the descendants of these animals, as indicated by the dotted lines, the facio-cranial indices are widely divergent; in the Titanotheres (*Brontotherium*) the cranium is elongated; in the horses (*Equus*) the face is elongated.

cephaly of the Alpine type, recalling the broad-headed Asiatic type of skull. Thus (Ripley, p. 56) "pure physical types come in contact and this means ultimately the extinction of extremes." Applying these principles to the present case, it implies the ultimate blending of the long and the narrow heads and the substitution of one of medium breadth.

Elliot Smith also (letter, August 12, 1911) implies a gradual modification or blending of head form through prolonged intermixture. He observes:

> Egypt does not give a clear answer to your queries because her exceedingly dolichocephalic brown race [related to the Mediterranean race of southern Europe] underwent a double admixture (circa 3,000 B.C.) with moderately brachycephalic "Armenoids" from Asia and dolichocephalic Negroes from Africa. The Mediterranean Egyptians are on the whole a little broader-headed than they were 6,000 years ago, and this *may* be due in part to a slow development toward mesaticephaly; but it is mainly the result of an admixture with alien bracephalics and mesaticephalics. There is an unquestionable tendency toward the elimination of the extremes of narrowheadedness and broadheadedness.

Hrdlička (letter, December 5, 1911) observes:

> As to the effect of the mixture of brachycephalic and dolichocephalic individuals or peoples, I am led to believe that there is in the results of such mixtures a large percentage of more or less intimate "blend" of the two forms, for such a condition is indicated by the curves of distribution of the cephalic index among such national conglomerates as the French, Germans, different tribes of the American Indians, etc. These curves, if sufficiently large numbers of individuals have been examined, all approach more or less the ideal camel-back curve. If no "blend" existed, we should be bound to get the double or dromedary-back curve. Of course the effects of mixture and the effects of environment are with our present means often impossible of separation, they often obscure each other. Yet the indications are that there is generally a considerable amount of more or less mixture of the many elementary constituents of the hereditary characters [known collectively as] dolichocephaly and brachycephaly. With this there coexists doubtless some tendency toward a differentiation into the two opposite forms of the head.

Thus in human head form we have proofs of continuous

allometric change strictly comparable to that which occurs in the crania of lower mammals, especially as observed in the horses and titanotheres; the extremes are produced in so-called pure human races under geographic isolation; when these pure races are brought together there arises disharmonism or alternating heredity or both. Neither the dolichocephalic nor brachycephalic type is as yet known to be dominant; opinion is divided as to whether in the first cross the heredity is pure or whether there may be a tendency to produce an intermediate form; opinion is nearly unanimous that prolonged interbreeding produces blends.[36]

4. *Skull of Titanotheres.*

The continuity of allometric evolution in the skull of the titanotheres (Fig. 4) has been the subject of prolonged investigation by the writer, assisted by Dr. W. K. Gregory, involving thousands of measurements, many of which belong in strictly successive phyletic series. Allometry (*i. e.*, the measurement of allometrons) here applies to the skull as a whole. We secure the cephalic index by dividing the breadth across the cheek arches by the total basilar length of the skull. There are also other indices, such as the facio-cranial, in which we measure continuous trends of allometric change; brachycephaly and dolichocephaly arise independently in four different phyla or lines of descent. The adaptive significance is sometimes apparent, sometimes obscure. As shown in Fig. 1 the titanotheres, like man, exhibit facial abbreviation and cranial elongation (postopic dolichocephaly) in contrast with the facial elongation (proopic dolichocephaly) of the horses. These phenomena are similar to those of cytocephaly, or the bending down of the face upon the base of the cranium as observed in the reindeer

[36] T. H. Morgan observes that a blend may occur in the first generation, F_1, even where perfect segregation occurs in F_2. The results of crossing the equine skull as described below indicate a tendency to blend in the first cross.

(*Rangifer*) and the hartebeest (*Bubalis*). Cytocephaly is an ontogenetic and phylogenetic new character, arising or developing continuously.

As in the case of the human skull, the causes of these profound changes in head form are entirely unknown; the mechanically adaptive significance is sometimes apparent, sometimes obscure. The evidence is strengthened by the examination of the titanotheres that human selection has little or no influence on human cranial form. The great point to emphasize is that *this allometric evolution in the skull and all parts of the skeleton is the prevailing phenomenon of change in the skeleton of mammals.* It is constantly in progress and is universally, so far as we can observe, a continuous process. As displayed in the four phyla of titanotheres (Fig. 3), the elongation or broadening of the foot bones proceed independently and are *divergent,* while in the same mammals the rectigradations exhibited in the rise of similar cusplets on the teeth and similar horn rudiments on the face are *parallel;* in the former case no ancestral predisposition seems to be operating, in the latter case ancestral predisposition certainly seems to operate; this is why the internal laws controlling the origin of new allometrons and of new rectigradations and allometrons are regarded as essentially dissimilar.

Paleontological analysis of these rectigradations and allometrons even unaided by experimental heredity reveals the essential feature of the "unit character" principle, namely, *that what we are observing is an incredibly large number of unit elements each of which enjoys a certain independence of evolution at the same time that each unit is adaptively correlated with all the others.* For example, in the upper and lower grinding teeth of horses alone there are 504 cusp units, each of which has an independent origin and development; at the same time each cusp is more or less distinctly correlated in form with the all-pervading dolichocephaly or brachycephaly of the skull; in fact, from certain single cusps of the teeth we

can often determine whether the animal is brachycephalic or dolichocephalic.

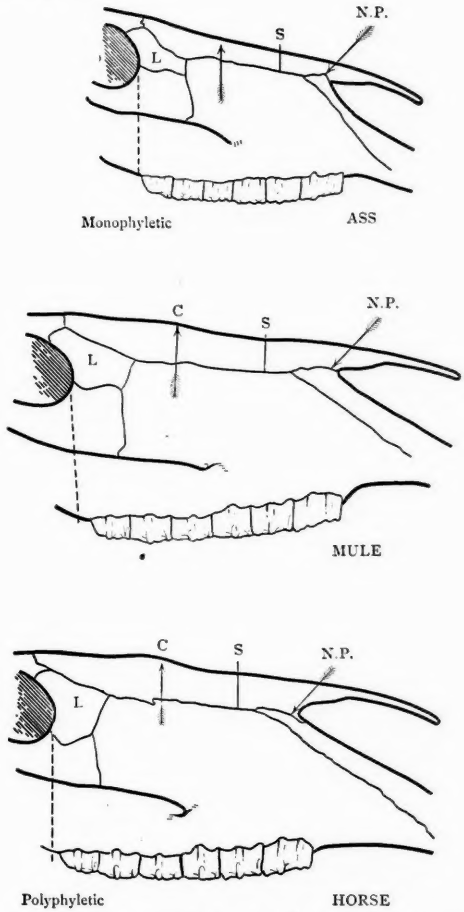

FIG. 5. CROSS-BREEDING AND IMPERFECT BLENDING OF ALLOMETRIC "UNIT CHARACTERS" OF THE FACIAL BONES IN ASS (MALE), HORSE (FEMALE) AND MULE.

Bones of the side of the face, Ass.
Bones of the side of the face, Mule.
Bones of the-side of the face, Horse.

The horse is certainly polyphyletic, the ass is probably monophyletic. *C.* The arrow points to *C*, a distinct bump in the horse and mule, not observed in the ass. *S* = point at which the section of the nasals is taken. *L* = lachrymal. *N.P.* = naso-premaxillary suture.

The question arises as a result of the somewhat conflicting evidence as to the crossing of brachycephals and dolichocephals in man, what happens when we cross two phyla of lower mammals which have been diverging along separate allometric lines and in the meantime have acquired a greater or less number of new characters which when sufficiently developed attain specific rank.

The answer is given very distinctly in the cross between the dolichocephalic horse (*E. caballus*) and the mesocephalic ass (*E. asinus*). Here we learn again that profound differences have been established through continuity and that we are enabled to split up these differences into distinct or partially blending units through cross breeding.

5. *Blended or Alternating Heredity in Horses.*[37]

So high an authority as J. Cossar Ewart (1903) has sustained the prevailing view that in the mule there is generally an imperfect blending of the characters of the immediate parents; the same author, however, notes that mules occasionally serve as examples of unit or exclusive inheritance.[38] He cites two cases: (1) a mule out of a well-bred, flea-bitten New Forest pony closely resembles her sire, the ass; (2) a "calico" mule, on the other hand, is surprisingly like his dam, an Indian "painted" pony. This painted mule demonstrates that the ass is not always more prepotent than the horse. From this author's very extensive breeding experiments the following conclusions are reached: the less fixed or racially valuable characters

[37] The writer is indebted to Mr. S. H. Chubb, Mrs. Johanna Kroeber Mosenthal and to Dr. W. K. Gregory for many of the observations and all of the measurements on which this comparison is based. The materials studied are three skulls of the ass (♂ *E. asinus*), ten of the horse (♀ *E. caballus*), and four of the mule, all adult with teeth in approximately the same stage of wear.

[38] The most recent (1912) opinion of Ewart is much more positive as to the operation of Mendel's law in pure breeding strains of horses. See "Eugenics and the Breeding of Light Horses," *The Field*, February 10, 1912, pp. 288, 289.

of zebras either blend with or are dominated by the corresponding characters in their horse and ass mates. Thus, as influencing dominance or prepotency, the value which a character has attained in the past struggle for existence seems to count for something. In zebras and in horses certain physical and mental traits are more highly heritable than others. Among the characteristics which are often handed down unblended in zebra-horse hybrids and to a less extent in zebra-ass hybrids are the size of the ears, the form of the hoofs, the massiveness of the jaws; while among psychic characters are transmitted the extreme caution, the wonderful alertness and quickness.

The new results brought forward in this Harvey lecture from the comparison of the skull and teeth of the horse, ass and mule on the whole strengthen the theory of unit inheritance both in rectigradations and in allometrons. The measure of unit character inheritance as contrasted with blended inheritance is very precisely brought out in the detailed study of the twenty-two characters which are examined below. Before discussing these characters in detail it is interesting to point out that the ancestors of the horse and the ass have probably been separated for at least 500,000 years. In the meantime the horse has become extremely dolichocephalic, the ass has remained comparatively mesocephalic; the horse has a relatively long, the ass a relatively short face; the horse has highly complex, the ass has somewhat simpler grinding teeth; the horse exhibits advanced adaptation to grazing habits and has become habituated to a forest and plains life in comparatively fertile countries, while the wild ass is by preference a browsing animal, finding its food in excessively arid countries where there is a marked dearth of water and water courses. The physical and psychical divergences in these two animals have developed over an enormously long period of time. Every single tooth and bone of the horse and ass show differences both in rectigradation and in allometric evolution.

One feature which tends to make the results of the cross less clear and distinctive than they are is that while the ass is monophyletic (being descended with

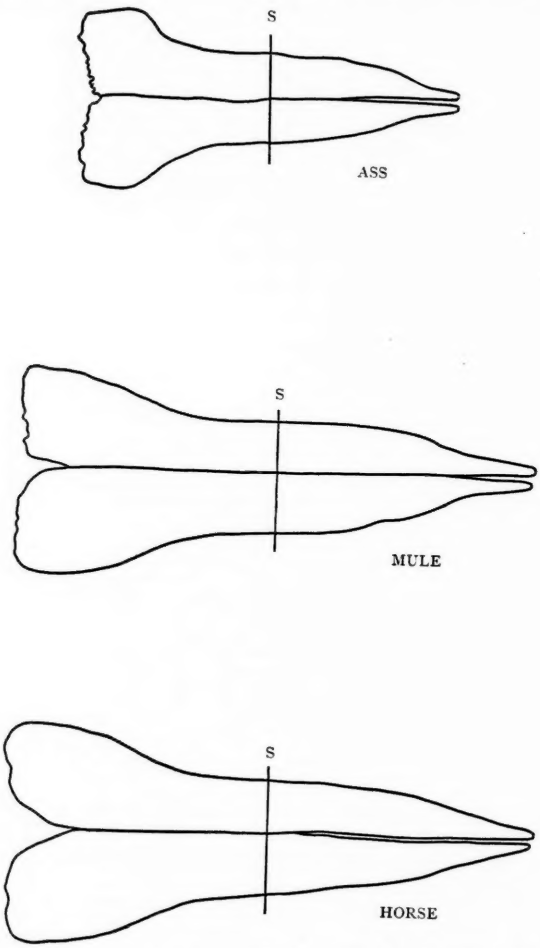

FIG. 6. CROSS-BREEDING AND IMPERFECT BLENDING OF SUB-ALLOMETRIC "UNIT CHARACTERS" OF THE NASAL BONES IN ASS (MALE) AND HORSE (FEMALE).

Top view of nasals and naso-frontal suture, Ass.
Top view of nasals and naso-frontal suture, Mule.
Top view of nasals and naso-frontal suture, Horse.
S = point of section shown in Figs. 3 and 5.

modification from the wild *E. asinus* of northern Africa), the domestic horse is not a pure strain and is certainly polyphyletic, having in its blood that of several races, such as the Arab and the Forest or Norse horse, animals which have specific distinctness although they still interbreed.[39] To this mixed strain or polyphyletic heredity of the horse, are probably attributable many of the allometric variations in the bones of the skull and in the enamel pattern of the teeth of the mule in some of which we observe a nearer approach to the ass type than in others. If we could cross the ass with a pure horse race like the Steppe or Prjevalsky horse we should probably obtain more precise results. Another disturbing feature in the comparisons and indices given below is that we do not know the exact structure of the skull of either of the parents from which the mule skulls examined were derived.

Despite these sources of fluctuation and of error, the general results obtained are fairly positive and definite.

The first point of interest in the segregation of unit characters in the mule is that connected with the *three germinal layers,* namely, the epiblast, mesoblast and hypoblast. All the characters of epiblastic origin appear to be derived from the sire, namely, the epidermal derivatives, the distribution of the hair, especially in the mane and tail, the hoofs, etc., are those of the ass, although the color pattern, as in the "calico" mules described by Ewart, may be derived from the mare. The nervous system and psychic tendencies, all of epiblastic origin are also derived from the ass, including minor psychic characteristics, such as aversion to water. Still more striking, perhaps, is the fact that the enamel pattern of the grinding teeth, again of epiblastic origin, is mainly that of the ass, although, as shown below, there are some intermediate and some distinctive horse-like characters in the

[39] There are many absolute characters which separate the Arab from the Norse horse, among them the invariable presence of one less vertebra in the lumbar region of the back.

teeth of the mule; this may be partly connected with the mesoblastic derivation of the dentine of the teeth.

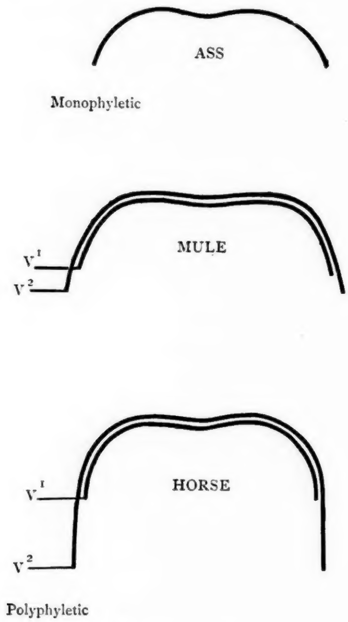

Fig. 7. Cross-breeding and Imperfect Separation of Allometric "Sub-unit Characters" of the Nasal Bones in Ass (Male), Horse (Female) and Mule.

Mid-section of nasal bones, Ass.
Mid-section of nasal bones, Mule.
Mid-section of nasal bones, Horse.

V^1, V^2 = variations in the depth of the nasals in the mule. V^1, V^2 = variations in the depth of the nasals in the horse.

Mesoblastic derivatives, on the other hand, are divided between the sire and dam, the skeleton and limbs of the mule being mainly proportioned as in the ass, while the skull of the mule, as we shall see, is almost purely that of the horse.

Blended and Pure Inheritance in the Bones of the Face

Blending.—A comparison of the bones of the side of

the facial or preorbital region shows intermediate or partly blended form and proportions both of the *nasals, premaxillaries, frontals,* and *lachrymals,* in which, however, the mule approaches *E. caballus* rather than *E. asinus.* Attention may be called to some of the details of the comparison: (1) *Suture between the nasals and premaxillaries:* in *E. asinus* short and elevated, in the mule intermediate but more like the horse; in the horse elongated and depressed (see Fig. 5). (2) *Naso-frontal suture on the top of the skull:* in the ass straight or transverse; in the mule incurved, more like the horse than the ass; in the horse arched or incurved (see Fig. 6). (3) *Depth and convexity of the nasals:* in the ass shallow and flattened; in the mule deeper, more like the horse; in the horse highly arched. (4) *Bump or convexity on posterior third nasals:* in the ass very slight; in the mule moderate, more like the horse than the ass; in the horse strong (see Fig. 7).

The same tendency in the mule to exhibit a slight departure from the horse toward the ass type is shown in the outlines of the bones of the face (Figs. 3, 4, 5). Comparing step by step the premaxillaries, maxillaries, nasals, and lachrymals, while the proportions and the sutural outlines are mainly those of the horse, there is a more or less distinct blending, or intermediate character in the direction of the ass; see especially the naso-premaxillary suture, the degree to which the nasals extend downward on the sides of the face to join the maxillaries, and the degree to which the nasals extend on the sides of the face to join the maxillaries. In this naso-maxillary junction certain horses approach the ass type. The characteristic bump on top of the nasals of the horse is transmitted to the mule, and the highly characteristic transverse suture between the frontals and the nasals, as seen from the top (Fig. 4), is rather that of the horse than of the mule.

Non-blending.—More definite results are shown in the heredity of the indices or ratios between the various por-

tions of the skull and of the teeth; these indices are extremely constant allometric specific characters, they are independent of size. For example, the indices of a diminutive pony and of a giant percheron would be the same. Similarly the indices of a diminutive donkey and of a very large ass would be the same.

The index is the best and most exact form of expressing mathematically the profound differences between the skull of the horse and that of the ass. Indices have the value of specific characters; they are of especial significance in the present discussion in comparison with those in the face, cranium and palate of man and of the titanotheres above considered.

Chief among the allometric differences are the following: (1) In its proportions the ass has a relatively shorter space between its grinding and its cutting teeth, the bit-opening; this is correlated with the fact (2) that the ass has a relatively broader and shorter skull than the horse; also with (3) the fact that the ass has a relatively longer cranium (postorbital space) and shorter face (preorbital space) than the horse; (5) the ass also has relatively broader grinding teeth correlated with the broader skull; (6) correlated also with its less elongate skull the ass has a relatively rounder orbit than the horse, *i. e.*, the vertical and horizontal diameters are more nearly equal. (7) A very distinctive feature is the angle which the occiput makes with the skull; this is one of the marked specific features of the ass.

NON-BLENDING OR PURE INHERITANCE INDICES IN THE SKULL

1. Cephalic Index:	$\frac{\text{Width of skull} \times 100}{\text{Basilar length}}$	Ass	46.9–49.9
		Mule	40.8–43.6
		Horse	40.4–44.1
2. Diastema Index:	$\frac{\text{Diastema} \times 100}{\text{Basilar length of skull}}$	Ass	15.6–17.6
		Mule	18.6–21.9
		Horse	18.2–23.0
3. Cranio-facial Index:	$\frac{\text{Length of cranium} \times 100}{\text{Length of face}}$	Ass	56.3–61.0
		Mule	48.9–51.8
		Horse	45.3–49.9

4. Orbital Index:	$\frac{\text{Vertical diameter of orbit} \times 100}{\text{Horizontal diameter}}$	Ass Mule Horse	96.0–104.2 78.7– 99.1 84.2– 93.5
5. Molar Index:	$\frac{\text{Transverse diameter of } M^2 \times 100}{\text{Total length of entire molar series}}$	Ass Mule Horse	15.2–16.0 14.2–14.9 13.9–15.7
6. Occiput-vertex angle Index:	Angle between vertex of skull and line connecting most posterior points of occipital crest with condyles, *i. e.*, nearly all horse skulls will stand when set up on end, some mule skulls (one out of four), no ass skulls	Ass Mule Horse	52.5–60.0 61.0–66.5 64.0–76.5
7. Vomer Index:	$\frac{\text{Distance from palate to posterior end of vomer} \times 100}{\text{Distance from vomer to foramen magnum}}$	Ass Mule Horse	93.8–111.7 95.5–110.3 72.8– 86.5

The above indices prove that the mule has not a primitive skull like that of the ass on a larger scale, but has essentially the skull of the horse, namely:

1. A long, narrow skull, as a whole.
2. A long diastema, or space for the bit.
3. A short cranium and a long face.
4. A long, oval orbit.
5. A relatively elongate and narrow set of grinding teeth.
6. A vertically placed occiput.

The one character in which the mule resembles the ass is the elongation of the vomer behind the bony palate. It should, however, be distinctly stated that while the indices given above are those which probably prevail in mules, there are overlaps in the (4) orbital index and (6) occiput-vertex angle. Thus in one mule the orbital index agrees with that of one of the asses.

Enamel Pattern of Grinding Teeth.—In the marvelously complex pattern of the grinding teeth the "unit character" transmission is quite sharply defined in the majority of characters, while intermediate or slightly blended in the minority. In general in the grinding teeth of the ass the main enamel folds are less complicated

than in the horse and there are fewer secondary or subsidiary folds; the ass especially lacks the "pli caballin" (fold 5) which is usually a very pronounced specific character of the horse. The mule shows a very slight indication of this fold and thus resembles the ass. The

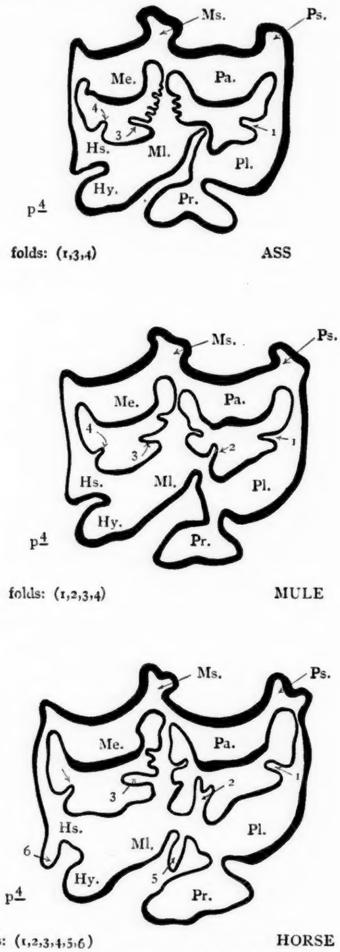

FIG. 8. CROSS-BREEDING AND SEPARATION OF RECTIGRADATIONS, DISTINCT "UNIT CHARACTERS" IN THE ENAMEL FOLDINGS AND PATTERN OF THE GRINDING TEETH OF THE ASS, MULE AND HORSE. Section through the crown of the third superior grinder (p^4 or 4th premolar) ass (male), horse (female) and mule.

subsidiary folds in the grinders of the mule are simpler than those in either the horse or the ass. The grinder of the mule would be pronounced by any systematist not knowing its mixed parentage to belong to the ass rather than to the horse, especially in the absence of the "pli caballin" (fold 5), in the form of the hypostyle (*hs*, fold 6), in the smaller size of the protocone (*pr*), the large size of which is very distinctive of the horse. A very detailed study and comparison of the grinding teeth in the horse, ass and mule made by an independent observer, Dr. W. K. Gregory, gives the following result:

Secondary folds:	protocone,	*pr.*					
	paracone,	*pa.*					
	metacone,	*me.*					
	hypocone,	*hy.*					
	protoconule,	*pl.*					
	metaconule,	*ml.*					
Secondary elements:	parastyle,	*ps.*					
	mesostyle,	*ms.*					
	hypostyle,	*hs.*					
Primary elements:							
	fold 1	......	Horse	......	Mule	......	Ass.
	fold 2	......	Horse	......	Mule.		
	fold 3	......	Horse	......	Mule	......	Ass.
	fold 4	......	Horse	......	Mule	......	Ass.
	fold 5	......	Horse.				

UNIT CHARACTERS IN GRINDING TOOTH OF THE MULE

Distinctly ass-like:	5 characters	11 peculiar to ass.
Less distinctly ass-like:	6 characters	
Common to horse and ass:	5 characters	5 common to horse and ass.
Distinctly horse-like:	2 characters	6 peculiar to horse.
Less distinctly horse-like:	4 characters	

It would be especially desirable to compare the same enamel characters in the hinny, which is a cross between the male horse and the female ass, in which it is well known that the *E. caballus* and *E. asinus* characters are differently distributed.

Summary.—Out of the 28 characters examined in the skull and teeth of the mule, 18 are distinctly derived either from one parent or the other with very slight, if any, tendency to blend, 10 characters show a distinct tendency to blend.

This evidence, in the opinion of T. H. Morgan, is in entire accord with the modern views of hybridizing; parallels for each instance can be given; without the evidence of the F_2 generation no conclusions adverse to Mendelism are possible. Even the differences in reciprocal crosses, *i. e.*, horse ♂, ass ♀, can be understood if sex-limited inheritance prevails in some characters.

To confirm the results suggested by this F_1 generation of the horse and ass, it would be necessary to interbreed races of mammals to F_2 or F_3 to ascertain whether these characters of the skull and teeth really mendelize. It is doubtful whether such specific types of mammals can be found, and whether sufficient stability of character exists in artificially produced races.

Sufficient evidence has been adduced, however, to show that a very large number of characters which are to the best of our knowledge of continuous origin, present all the appearance of "unit characters" in the first generation of hybrids.

III. Conclusion

Is it not demonstrated by this comparison of results obtained in such widely different families as the Bovidæ, Hominidæ, Titanotheriidæ and Equidæ that *discontinuity in heredity affords no evidence whatever of discontinuity of origin?*

As to origin, it is demonstrated in paleontology that certain new characters arise by excessively fine gradations which appear to be continuous. If discontinuities or steps exist they are so minute in these characters as to be indistinguishable from those fluctuations around a mean which seem to accompany every stage in the evolution and ontogeny of unit characters.

IV. Theoretical Considerations

After having attempted to confine our discourse to facts it is a pleasure to relax into the more genial atmosphere of opinion and hypothesis.

The principle of pre-determination, which results in the appearance of rectigradations, involves us in radical opposition to the opinions of the Bateson-DeVries-Johannsen school. There is an unknown law operating in the genesis of many new characters and entirely distinct from any form of indirect law which would spring out of the selection of the lawful from the lawless. This great wedge between the "law" and the "chance" conception, which since the time of Aristotle has divided biologists into two schools of opinion, is driven home by modern paleontology.

Paleontology, in the origin of certain new characters at least, compels us to support the truly marvelous philosophic opinion of Aristotle, namely:

Nature produces those things which, being continuously moved by a certain principle contained in themselves arrive at a certain end.

While recent biology has tended to sharply distinguish bodily from germinal processes and to place chief emphasis upon evolution appearing to originate in the germ cells, we must not forget that for a hundred million years or more, or from the beginning of life, the germ plasm has had both its immediate somatic and its more remote environmental influences. Because the grosser form of Lamarckian interpretation of transmission of acquired characters has apparently been disproved, we must not exclude the possibility of the discovery of finer, more subtle relations between the germ plasm and the soma, as well as the external environment. There are several phenomena, which have been observed only in paleontology, that afford evidence for the existence of such a *nexus;* because it appears that certain germinal predispositions to the formation of new characters, connected, as Darwin conjectured, in some way with community of descent, are only evoked under certain somatic and environmental conditions, without which they appear to lie in a latent, potential or unexpressed form.

All that we may be able to observe are the *modes* of

operation in the genesis of new characters and in the adaptive trends of allometric evolution without gaining any intimate knowledge of what the *causes* are. This thought may be made clear through the following analogy. Naturalists observed and measured the rise and fall of the tides long before Newton discovered the law of gravitation; we biologists are simply observing and measuring the rise and fall of the greater currents of life. It is possible that a second Darwin may discover a law underlying these phenomena bearing the same relation to biology that the law of gravity has to physics, or it is possible that such law may remain forever undiscovered. Another analogy may make our meaning still clearer. Ontogenesis is inconceivable, for example, the transformation of an infinitesimal speck of fertilized matter into a gigantic whale or dinosaur; we may watch every step in the process of embryogeny and ontogeny without becoming any wiser; in a similar sense phylogenesis may be inconceivable or beyond the power of human discovery. Not that we accept Driesch's idea of an entelechy or Bergson's metaphysical projection of the organic world as an individual, because we must believe that the entire secret of evolution and adaptation is wrapped up in the interactions of the four relations that we know of, namely, the germinal, the bodily, the environmental, with selection operating incessantly as the arbiter of fitness in the results produced. In the meantime[40] we paleontologists have made what appears to be a substantial advance in finding ever more convincing evidence of the operation of law rather than of chance in the origin and development of new characters, something which Darwin had clearly in mind.[41]

[40] Osborn, H. F., "The Hereditary Mechanism and the Search for the Unknown Factors of Evolution," Biol. Lect. Marine Biol. Lab., 1894, AMER. NATURALIST, Vol. XXXIX, No. 341, May, 1895, pp. 418–439.

[41] Darwin, Chas.: "I have spoken of variations sometimes as if they were due to chance. This is a wholly incorrect expression; it merely serves to acknowledge plainly our ignorance of the *cause* of each particular variation."

THE BIOLOGY OF THE CRAYFISH

F. E. CHIDESTER
Rutgers College

Introduction

The first reference to the crayfish in scientific literature is in Aristotle's "History of Animals," where he speaks of the "small Astaci which breed in the rivers."

Aristotle and the older naturalists used the term Astaci to include both the crayfish and the lobster.

Faxon divides the crayfish into two great groups (24): One, restricted to the northern hemisphere, is found in Europe, Asia and North America. The other is found in the southern hemisphere, in Australia, Tasmania, New Zealand, Fiji Islands, Madagascar and South America.

The islands now inhabited by crayfish, such as England, Japan and Cuba, were probably once connected with the mainland.

In speaking of the distribution of the crayfishes, Faxon says:

> The northern family of crayfishes contains two genera, *Astacus* and *Cambarus*. These groups occupy distinct geographical areas. The genus *Astacus* is found in the old world in Europe and western Asia as far as the Aral and Caspian Seas, and in America in the region west of the Rocky Mountains, draining into the Great Salt Lake and the Pacific Ocean. It is thus seen to occupy the western sides of the two northern continents. *Cambarus* is found in North America east of the Rocky Mountains, in the region which is bounded on the north by Lake Winnipeg and New Brunswick, and on the south by Guatemala and Cuba. Crayfish thus are discontinuous genera, that is, genera which now occupy widely separated areas, such as *Astacus* in Europe and Pacific North America, but which once ranged over the intervening ranges as well.

It is comparatively easy to distinguish the common *Cambarus* from the *Astacus* of Europe and western America. Members of the genus *Astacus* have eighteen

gills, while those of the genus *Cambarus* have but seventeen. The female of the genus *Cambarus* has a false pouch, the annulus ventralis, which serves as a sperm receptable, while in *Astacus* the sperm is deposited on the posterior part of the thorax in spermatophores.

Dr. A. E. Ortmann has made most careful studies of the distribution of the crayfish. References to his papers will be found in my bibliography. Dr. Ortmann writes me that there are in the United States and Central America, 74 species of *Cambarus* and 5 of *Potambius* (*Astacus*). In the United States excluding Mexico, Guatemala and Cuba, there are 64 species of *Cambarus* and 5 of *Potambius.*

The European word "crayfish" is used by teachers of zoology, probably because of Huxley's classic, "The Crayfish."

Ortmann found (38) that not only was "crawfish" used by Say, 1817, earlier than "crayfish" by Huxley, 1880, but that in this country "crawfish" is the popular name.

"Crayfish," "crawfish," or, as it is sometimes incorrectly called, "crab," come from the same root, Old German, "Krebis," from which are derived, on the one hand, the modern German " Krebs " and the English " crab "; on the other hand the French " ecrevisse," the English and the American " crayfish."

The crayfish on which my own observations have been centered belong to the species *Cambarus bartonius bartoni,* the only species which has migrated into New England.

My work was carried on in the field and in the laboratory continuously for nine months. In the field I have watched the activities of the crayfish in the small ponds with which Worcester, Mass., is so well supplied. At night I used a powerful acetylene gas lamp. In the laboratory I made use of two large aquaria, one of them an ordinary running water aquarium with a pile of sand at

one end, and the other a still water aquarium arranged to furnish a more nearly natural habitat.

In this paper I have not touched upon the anatomy or the work on regeneration, but have confined myself to what is generally known as ecology or biology. In the attempt to make the paper fairly complete I have referred in the text to the numbers in the bibliography.

It is a pleasure to acknowledge my indebtedness to Dr. C. F. Hodge, Dr. Newton Miller and Dr. J. P. Porter, of Clark University, Dr. A. E. Ortmann, of the Carnegie Museum of Pittsburgh, and Dr. E. A. Andrews, of Johns Hopkins University.

Senses

Touch.—Touch is probably the sense of greatest value to the crayfish. It is sensitive to touch over the whole surface of the body (16), especially on the chelae and chelipeds, mouth parts, the ventral surface of the abdomen and the edge of the telson.

Vision.—The crayfish, in common with the insects, has a compound eye. It is believed by many that the compound eye is a visual apparatus which is almost worthless for detecting the forms of objects, especially if these objects are stationary; but that it may furnish a very definite response to stimuli of moving objects.

Bell's experiments with the crayfish (16) showed that there was no response to stationary objects. The case was entirely different with large, moving objects. The response was not due to any change in the intensity of light such as that caused by a shadow falling on the animals, for they would react to a movement made on the opposite side of them from the window. Reaction to smaller moving objects was not so marked.

Crayfish are sensitive to strong light and hide during the day under stones, among roots of plants near the bank, and in burrows in the bank. It is a noteworthy fact that, in France, the people catch crayfish by building huge fires on the bank at night to attract them.

My own experiments indicate that in nature the crayfish will retreat from a strong light, but will approach a dim one. In the spring I found that it was extremely difficult to frighten a crayfish from its food by means of my acetylene light. In collecting at night it is very easy to attract crayfish from some distance by setting a light on the bank so that it dimly illuminates some little space of water.

Smell and Taste.—Very little experimental work to determine the senses of smell and taste in any of the crustacea was done until Bell, in 1906, tested the reactions of the crayfish (15) to chemical stimuli, applying meat juice by means of a fine pointed pipette to various parts of the body. He found that the antennæ, antennules, mouth parts and chelipeds were especially sensitive.

Recently (1910) Holmes and Homuth published the results of an extended series of experiments on crayfish in which the outer or inner rami of the antennules were removed; the antennules were removed entirely; the antennæ were removed; the chelipeds removed; and in some specimens the brains were destroyed (33).

They found that the outer rami of the antennules bearing the olfactory setæ were especially sensitive to olfactory stimuli, that the inner rami of the antennules, the antennæ, the mouth parts and the tips of the chelipeds were all sensitive to some extent to olfactory stimuli.

It is probable that in the crayfish we have a very highly developed topochemical sense, or contact-odor sense. Forel uses this term (25) in speaking of the fact that in ants, odors are apparently detected by the contact of the antennæ.

Bell found that the crayfish was sensitive to food when *not* in contact with it. I experimented with freshly cut meat and with meat which had been exposed to the air for some time so that the cut surfaces had dried, and found that the crayfish would go toward and seize the fresh meat first. Evidently the diffusion of the meat juices was readily detected.

Hearing.—It has been pretty clearly demonstrated by Bell that the crayfish has no sound reactions. He tried experiments (16) such as rapping on a board floating in the water, snapping a metal snapper in and out of the water, and setting tuning forks in vibration in the water, but got no response.

It is possible that the crayfish is sensitive to the sound made by the movement of the *mouth parts* of another crayfish. This has not been proved.

Equilibrium.—Bunting found that young crayfish with the statocysts removed would swim upside down as readily as right side up (18). It is also pretty certain that the older crayfish have a sense of equilibrium, although the response to rotation in their case is not definite, but purely individual.

Mating, Spawning and Development.

The process of mating in *Astacus* differs from the process in *Cambarus*. In the case of *Astacus*, the males approach the females in October, November and January.

> The male seizes the female with his pincers, throws her on her back and deposits the spermatic matter, firstly on the external plates of the caudal fin, secondly on the thoracic sterna around the external openings of the oviducts. During this operation the appendages of the first two abdominal somites are carried backwards, the extremities of the posterior pair are enclosed in the groove of the anterior pair; and the end of the vas deferens becoming everted and prominent, the seminal matter is poured out and runs slowly along the groove of the anterior appendage to its destination, where it hardens and assumes a vermicular aspect (20).
>
> After an interval of from ten to forty-five days, oviposition takes place. The female rests on her back and bends the abdomen forward, forming a chamber into which the oviducts open. The eggs are passed into the chamber by one operation, usually during the night, and are plunged into a viscid, gray mucus with which it is filled. The spermatozoa pass out of the spermatophores and mix with this fluid, fertilizing the ova, but just how, and what becomes of them, are unknown (20).

The female of *Cambarus* differs from the female of *Astacus* in having a false pouch, the annulus ventralis. Andrews found that this pouch does not appear in *Cam-*

barus affinis until the individual has reached a third stage after leaving the egg.

The method of sperm transfer in *C. affinis,* and that of *C. b. b.* as well, is as follows:

The male everts the bent, nozzle-like papillæ at the mouth of the vasa deferentia and through them discharges sperm into an actual tube that passes down each of the first two abdominal appendages or stylets. Both first and second pairs of stylets are locked together by a peg and groove contrivance. The sperm thus passes through a closed tube from the vasa deferentia into the annulus ventralis without coming into contact with the water. Copulation lasts from two to ten hours and may be repeated by either animal with some other (3, 4).

In a previous paper, I pointed out (21) that the males do not distinguish the females and that males "repeatedly grasp other males, and sometimes, in spite of their frantic struggles turn them over and attempt to copulate with them." The crayfish is at such a state of nervous tension during the period of sexual activity, that the female will curl her abdomen at the slightest touch and the male will at first grasp any rounded object presented to him and attempt to overturn it. A stimulus so slight as the slow lowering of the water when I siphoned it from the closed tank, was sufficient to cause violent activity among the males, with the result that all the females were soon held by males.

Pearse, in a study of crayfish made in the laboratory with no attempt to reproduce natural conditions (40), has made many interesting observations and experiments, verifying my statements (21) and adding the discovery that a male will copulate with a dead female. He discovered that the male of one species had succeeded in adjusting his stylets to the annulus of a dead female of another species.

Andrews has just published a paper (13) in which he mentions seeing males attempt to copulate with dead and bound or paralyzed males and to actually go through all the activities of mating with dead females except the injection of the spermatophores and plugging of the annulus. He agrees with my previous statement that the males

do not recognize the females, and suggests that the difference from the standpoint of the crayfish between the sexes is a difference of behavior, which difference is perceived by muscle and touch sense.

The passivity of the female when seized is marked in the crayfish, but as I shall show in another paper, in the marine crabs the female is not passive but aids in the movements preliminary to conjugation.

It is possible, though I have not at present enough observations to support the theory, that in the crayfish and the lobster, deposition of sperm is most effective when the female has just moulted and the annulus ventralis or the ventral surface, as the case may be, is clean. In crabs where fertilization is internal, it is necessary that the shell be soft; softness is of course of no use where the fertilization is external, in fact it might be injurious; but the cleanness of a new coat may facilitate the deposition of the spermatophores, and the retention of the plug.

Anatomically there should be no difficulty in crossing the different species of *Cambarus*. It would be interesting to see if spermatophores deposited by a male *Astacus* on the shell of a female *Cambarus* would fertilize the eggs. It is quite probable, however, that the female would not leave the spermatophores on her thorax and abdomen until the time of egg extrusion.

Andrews (13) transplanted sperm receptacles of several females to females of another species and the mutilated females lived to lay eggs but the eggs did not develop. Males would not fill the transplanted receptacles. Andrews found that conjugation between species may take place to some extent, but did not succeed in any case in securing sperm transfer and actual crossing of species.

There seems to be no well-marked mating season in the cold-water species, including the species on which my observations were made. In the ponds, mating crayfish were not found later than November 1, but in the laboratory copulation occurred at intervals during the fall,

winter and spring. It is probable that in its native haunts the crayfish behaves differently.

In the spring the males die off in great numbers. This is a phenomenon which is noted in many arthropods, and seems to be a wise provision of nature to prevent the now useless males from using up the food required for the spawning females and the young crayfish. Some of the males, however, live to a good old age. I have found several that were over 90 mm. long.

In the case of *C. bartonius bartoni* there are two more or less well-marked spawning seasons, fall and spring.

The fall laying, as indicated by females brought into the laboratory, is during the latter part of September and all through October and November. The spring laying extends from about March 15 to about May 15.

Andrews observed the process of laying in *Cambarus affinis.* For four or five days previous to laying, the female cleans her abdomen diligently and is exceedingly sensitive to disturbances during that time. The actual laying is done in deep water at night. It takes from ten to thirty minutes to extrude the two hundred to four hundred eggs. Each egg is attached by a tiny filament to the abdominal hairs (9).

The time of fertilization is supposed to be when the eggs are laid, as they pass over the annulus ventralis. Andrews found that on the removal of the annulus before the eggs were extruded, the eggs were unfertilized and did not develop.

When first extruded the eggs are almost black, but as development goes on they become reddish in color and at the end of about four weeks, when the young crayfish are hatched, they are nearly transparent. The time of development, from the extrusion of the eggs till the crayfish are detached from the parent, is about eight weeks in the species which I studied.

Even after the young are detached from the swimmerets of the mother, for several days they do not venture far from her, and taking warning at any apparent danger,

scuttle under her abdomen. It is probable that here the visual sensitivity to moving objects is more highly developed than in the adult in comparison with other senses.

The young crayfish moults very frequently during the first year.

I found that two or three days before moulting the adult crayfish come up into the shallows exposing their carapaces and drying them out thoroughly. The first time that I saw this prolonged drying-out process I did not think it significant, for I have seen crayfish in ponds where the water was pure and fresh, elevating their carapaces for a few minutes at a time. It is a habit which is not necessarily caused by impure water, for the same thing was noted by me in the laboratory with animals in the running-water tank.

When I noted by the number (in oil paint) on its back that the same individual was continually remaining only partly submerged, I made a note and watched developments. Later, in three other crayfish I noted this preliminary drying out, and predicted the approximate time of the moults. This was convenient knowledge, for a crayfish in difficulty with his half removed old coat falls easy prey to his brethren.

It is possible that the aeration of the attached young by the mother is for the purpose of enabling the young crayfish to moult more readily. Observations like these have not been reported for other crayfish or for marine crustaceans, but it seems possible that in the crayfish we have such a drying out of the old exo-skeleton as we find taking place in insects, like the dragon fly, which live for a time in the water.

Andrews made a thorough study of the young of both *Astacus* and *Cambarus* and found that in *Cambarus* the young four months old averaged about 41 mm. in length. During the winter of the first year there is no increase in size, but the second summer of life marks an increase of thirty per cent. in length (12).

I have found females but one year old with eggs, and the development went on in the laboratory just as in the more mature females. The largest female that I captured was 102 mm. in length. The largest male was 90.5 mm. long.

FOOD.

Crayfish are omnivorous. I have previously shown that *C. bartonius bartoni* prefers fresh animal food to stale animal food or either fresh or stale vegetable food (21).

Some crayfish eat a great deal of vegetable matter, one species, the chimney builder, *Cambarus diogenes,* seeming to prefer it. The vegetable matter eaten consists of dead leaves, potato, onion, young corn and buckwheat.

The animal food consumed by the crayfish consists of worms, insects, insect larvæ, a few fish, frog, toad and salamander eggs, and occasionally a dead fish or frog. I have seen crayfish devour a hapless relative who was endeavoring to rid himself of his old shell. Sometimes females eat eggs from their own abdomens and even devour their own freed offspring.

Enemies.—The crayfish suffers from internal and external enemies. Among the plants which live symbiotically with the crayfish are diatoms, bacteria and saprolegnia. Internally, *Distoma cerrigerum* and *Branchiobdella* have been noted. But these are not all the enemies of the crayfish. Besides man, who uses thousands of dollars worth of crayfish for food and as a garnish, many small animals find them palatable.

Many fish, including the black bass, *Micropterus,* which fishermen find very partial to crayfish, eat them.

Professor Surface reported (38) that the salamanders *Cryptobranchus allegheniensis* and *Necturus maculosus,* are among the chief enemies of the crayfish.

Ortmann mentions seeing the water snakes, *Natrix sipedon* and *N. lebens,* when captured, disgorge crayfish

and has also found garter snakes, *Eutænia sirtalis,* in the holes of *Cambarus monongalensis.*

In the laboratory and in the field I have found that the common box turtle catches many crayfish.

Many birds, including the eagle, king-fisher, wild ibis and turkey, have been observed with crayfish in their claws; or the remains have been seen at the nests.

Crayfish as Injurious Creatures.

The river species do not especially injure human interests except in occasionally capturing a few toads, fish and frogs, but the burrowing species are cited by Ortmann (38) as being very injurious, especially in the lowlands of Pennsylvania, Maryland and West Virginia.

They make mud piles which clog harvesting machines, and are considered by the farmers in Maryland as such pests that it is common to throw unslacked lime over the fields in order to kill the unwelcome tenants.

West Virginia farmers claim that the crayfish destroy crops of buckwheat, corn and beans by eating the young sprouts.

Great damage is done by the burrowing species *Cambarus diogenes,* in burrowing into dams on ponds and reservoirs, one notable instance being the levees of the Mississippi (38).

To destroy crayfish it is customary to throw unslacked lime over the fields, or to pour carbon bisulphide into the holes, or to drain the infested area.

None of these measures is efficacious, the first two methods being impracticable on account of the difficulty in reaching the bottom of the burrow and the second, simply lowering the water level, only delays matters a little.

Value of the Crayfish.

At the present time, with the lobster fishery in a state of decline, it seems as if the crayfish could be profitably substituted for its larger cousin.

In a carefully written paper (11) Andrews sets forth the possibilities of crayfish propagation.

He states that, from the small region on the Potomac between Washington and Fort Washington, it was estimated that there were half a million crayfish sent annually to New York.

New York, New Orleans, Chicago, Milwaukee and San Francisco, and many other large cities consume large quantities as food.

In 1902, the U. S. Fish Commission reports state the crayfish catch of Monroe Co., Florida, was 55,664 pounds, worth $3,382.

In Oregon, 116,400 pounds, worth $7,760, were caught in one year.

With crayfish maturing in one season and growing to a length of from four to five inches in three years; and considering the large number of eggs (100–600) laid by one female, there should be but little difficulty in supplying a large demand for these animals.

When we consider that the large *Astacus* readily adapts itself to the slight difference in environment in the east, we see that the crayfish is a very practicable substitute for the lobster.

There should be no difficulty in disposing of the smaller *Cambarus*, either as fresh food or canned, as we get the abdomens of shrimps.

In the school and college laboratories, the anatomy of the crayfish has been studied ever since Huxley wrote "The Crayfish." The habits and activities of the young and adult crayfish are of great interest and profit for study. The animal is suited for many kinds of experiments, and the large ganglia and nerve cells are readily removed and are excellent for neurological work. The psychologists should find a profitable subject for study in the relations of mother and offspring for the few days just after the young are detached from the mother's swimmerets.

Daily Life.—From a lengthy series of observations,

including the continuous study of several specimens for twenty-four hours, I have concluded (21) that the crayfish shows his greatest activity at nightfall and at daybreak. In nature the crayfish is less active during the day than he is in captivity, since, as a rule, he has more hiding places in his natural habitat.

Pearse has stated (40) that the number of matings occurring in two boxes, one being painted black and closed entirely, and the other being exposed to light, did not vary to any extent. It is obvious from the work of Andrews and myself that the fact that crayfish in a state of sexual tension, stimulated by transference to different receptacles, copulate as well in the light as in the dark, does not bear on the question of normal activity. The difference between night and day must not be assumed to be entirely that of light, in experiments on higher invertebrates.

It is possible that the tendency of the crayfish to remain in hiding during the day is to some extent lessened when sexual feeling is strong, but this seems rather improbable under natural conditions.

In my specimens hibernation was well marked. I was careful to change the water daily in my still-water aquarium, thus keeping it fairly cool. Several of my crayfish hibernated as long as six weeks at a time, in closed burrows in the bank of this miniature pond.

BIBLIOGRAPHY

1. Abbott, C. C. '73. Notes on the Habits of Certain Crayfish. Am. Nat., Vol. 7, pp. 30–34.
2. Abbott, C. C. '85. How the Burrowing Crayfish works. *Inland Monthly.* Columbus, Ohio, Vol. 1, pp. 31–32.
3. Andrews, E. A. '95. Conjugation in an American Crayfish. Am. Nat., Vol. 29, pp. 867–873.
4. Andrews, E. A. '04. Breeding Habits of Crayfish. Am. Nat., Vol. 38, pp. 165–206.
5. Andrews, E. A. '04. Crayfish Spermatozoa. *Anat. Anz.,* Vol. 25, pp. 456–463.
6. Andrews, E. A. '05. The Sperm Receptacle of Cambarus. *J. H. U. Circ.,* No. 178, pp. 1–9.
7. Andrews, E. A. '06. Ontogeny of the Annulus Ventralis. *Biol. Bull.,* Vol. 10, pp. 122–137.

8. Andrews, E. A. '06. Partial Regeneration of the Sperm Receptacle in Crayfish. *J. Exp. Zool.*, Vol. 3, pp. 121–128.

9. Andrews, E. A. '06. Egg laying of Crayfish. AM. NAT., Vol. 40, pp. 343–356.

10. Andrews, E. A. '06. The Annulus Ventralis. *Boston Soc. of Nat. Hist. Proc.*, 5, 32, pp. 427–479.

11. Andrews, E. A. '06. The Future of the Crayfish Industry. *Science*, N. S., Vol. 23, pp. 983–986.

12. Andrews, E. A. '07. The Young of the Crayfishes Astacus and Cambarus. *Smithsonian Cont.*, Vol. 35, 79 p.

13. Andrews, E. A. '10. Conjugation in the Crayfish Cambarus affinis. *J. Exp. Zool.*, Vol. 9, pp. 235–264.

14. Bateson, W. '87. Notes on the Senses and Habits of some Crustacea. *J. Mar. Biol. Assoc. Un. King.*, Vol. 1, p. 211.

15. Bell, J. C. '06. The Reactions of the Crayfish to Chemical Stimuli. *J. Comp. Neurol. and Ps.*, Vol. 16, pp. 299–326.

16. Bell, J. C. '06. The Reactions of the Crayfish. *Harvard Ps. Studies*, Vol. 2, p. 615.

17. Brocchi, P. Traité de Zoologie Agricole. (Ecrevisse.) Pp. 702–720.

18. Bunting, M. '93. Ueber die Bedeutung der Otolithen-organe fur d. geotropischen Funktionen von Astacus fluviatilis. *Pflügers Archiv*, Bd. 54, S. 531.

19. Chantran, S. '70. Observations sur l'histoire naturelle des ecrevisses. *Compt. Rendu*, t. 71, pp. 43–45.

20. Chantran, S. '72. Sur la fecondation des ecrevisses. *Compt. Rendu*, t. 74, pp. 201–202.

21. Chidester, F. E. '08. Notes on the Daily Life and Food of Cambarus bartonius bartoni. AM. NAT., Vol. 42, pp. 710–716.

22. Dearborn, G. N. '00. Notes on the Individual Psycho-physiology of the Crayfish. *Am. J. Physiol.*, Vol. 3, pp. 404–433.

23. Faxon, W. '84. On the So-called Dimorphism in the Genus Cambarus. *Am. J. Sci.*, ser. 3, Vol. 27, pp. 42–44.

24. Faxon, W. '85. A Revision of the Astacidæ. Pt. 1: The Genera Cambarus and Astacus. *Mem. Mus. Comp. Zool.*, Vol. 10, pp. 1–186.

25. Forel, A. (Tr. by Yeardley, M, '07.) The Senses of Insects. London, 1907.

26. Garman, '89. Cave Animals from Southwestern Missouri. *Bull. Mus. Comp. Zool.*, Vol. 17, pp. 225–259.

27. Gulland, F. '06. The Sense of Touch in Astacus. *Proc. Royal Soc. Edinburgh*, Vol. 9, pp. 151–179.

28. Hay, W. P. '05. Instances of Hermaphroditism in Crayfishes. *Smithsonian Misc. Coll.*, Vol. 48, pp. 222–228.

29. Herrick, F. H. '95. The American Lobster. *Bull. U. S. F. C.*, pp. 1–252.

30. Holmes, S. J. '03. Death Feigning in Terrestrial Amphipods. *Biol. Bull.*, Vol. 4, pp. 191–196.

32. Holmes, S. J. '03. Sex Recognition Among Amphipods. *Biol. Bull.*, Vol. 5, pp. 288–292.

33. Holmes, S. J., and Homuth, E. S. '10. The Seat of Smell in the Crayfish. *Biol. Bull.*, Vol. 18, pp. 155–160.
34. Huxley, T. H. '78. On the Classification and Distribution of the Crayfishes. *Proc. Zool. Soc. London*, pp. 752–788.
35. Huxley, T. H. '80. An Introduction to the Study of Zoology, Illustrated by the Crayfish. Pp. 1–362. D. Appleton & Co., New York, 1895.
36. Jennings, H. S. '06. Behavior of Lower Organisms. Macmillan, 1906.
37. Lyon, E. P. '99. Contribution to the Comp. Phys. of Compensatory Movements. *Am. J. Physiol.*, Vol. 3, pp. 86–114.
38. Ortmann, A. E. The Crawfishes of the State of Pennsylvania. *Memoirs of the Carnegie Museum*, Pittsburgh, Pa., Vol. 2, pp. 343–523.
39. Ortmann, A. E. '05. The Mutual Affinities of the Species of the Genus Cambarus and their Dispersal over the United States. *Proc. Am. Phil. Soc.*, Vol. 44, pp. 91–136.
40. Pearse, A. S. '09. Observations of Copulation among Crawfishes with Special Reference to Sex Recognition. AM. NAT., Vol. 43, pp. 746–753.
41. Prentiss, C. W. '01. The Otocyst of Decapod Crustacea. *Bull. Mus. Comp. Zool. Harvard Univ.*, Vol. 36, p. 245.
42. Souberain, Leone. '65. Sur l'histoire naturelle et l'education des ecrevisses. *Comptes Rendus*, t. 60, pp. 1249–1250.
43. Tarr, R. S. '84. Habits of Burrowing Crayfishes in the United States. *Nature*, Vol. 30, pp. 127–128.
44. Washburn, M. F. '08. The Animal Mind. Macmillan, N. Y., 1908.
45. Weed, H. E. Carbon Bisulphide for Crayfish. Proc. Seventh Annual Meeting of Assoc. of Ec. Entom. U. S. Dept. of Ag., Div. of Entomol., Bull. 2, N. S., p. 100.
46. Wheeler, W. M. '10. Ants, their Structure, Development and Behavior. Columbia Univ. Press, New York, 1910. (Pp. 509–515.)
47. Williamson, E. B. '07. A Collecting Trip North of Sault Ste. Marie, Ont. *Ohio Nat.*, Vol. 7, pp. 129–148.
48. Yerkes, R. M., and Huggins, G. E. '03. Habit Formation in the Crawfish Cambarus affinis. *Harvard Ps. Studies*, Vol. 1, pp. 565–577.

PRESENT PROBLEMS IN SOIL PHYSICS AS RELATED TO PLANT ACTIVITIES[1]

PROFESSOR BURTON E. LIVINGSTON

THE JOHNS HOPKINS UNIVERSITY

IT is from the point of view of the physiologist and not from that of the analytical physicist that I propose here to consider some of the most obvious and insistent of the non-chemical problems of the soil. We shall thus be interested not in the physics of the soil, but in the *relation* of some of its physical properties to certain plant activities. This is a somewhat unusual point of view, for most soil investigators have studied the soil largely to the exclusion of the plant, bringing refined chemistry and physics to the statement of one member of the equation and stating the other member largely from the standpoint of the unscientific man. This generalization applies to studies upon both the physics and the chemistry of the soil, but, owing to the majesty of the great chemist Liebig[2] and to the multitude of his followers, soil physics has nowhere received the attention which it deserves, and the relation of the physical condition of the substratum to plant activities remains perhaps the most fundamental and at the same time most neglected of all the various environmental relations.

Since we are certain that the water relation is of exceedingly great importance in the control of plant processes, and since so many other physical soil conditions depend largely upon soil moisture, I shall consider here primarily only the water relation of terrestrial plants

[1] Presented in the Symposium on Problems of the Soil, before Section G, A. A. A. S., at the Washington meeting.

[2] Compare, in regard to the present contention, the title of Leibig's monumental work, "Die Chemie und ihrer *Anwendung* auf Agrikultur und Physiologie," 1846.

below the soil surface. But, as will shortly appear in some detail, to appreciate the problems before us it will be necessary, not only to deal with the internal conditions of the root system together with the external ones of the soil, but also to bear constantly in mind certain relations which obtain above the soil. I shall begin with a brief treatment of the water relations of *the plant,* with special reference to the physical conditions of its subterranean environment.

In order that the water content requisite for the various physiological processes may be maintained, the condition must obviously be fulfilled, that the ratio of *the rate of water income to that of water removal must never fall below unity.* Now, the removal of free water from the physiological system of the plant occurs in three general ways: (1) the fixation of water by growth, etc., (2) the excretion of liquid water at the periphery and (3) the loss of water vapor by transpiration. The first two of these are usually negligible, and the prime aerial condition of plant activity—as far as the water relation is concerned—is the rate of loss of water vapor. This loss is to a variable extent controlled by conditions within and without the plant, but we do not need to give these attention now. The main point for us to bear in mind is that, for the activities of the majority of terrestrial plants, it is requisite that the entrance of water through the roots must equal its rate of exit through the leaves and other aerial parts.

Of course water will not, in general, enter through the roots faster than it is removed from the plant body or fixed therein by growth and metabolism, and the critical consideration in respect to the soil water relation is not the actual rate at which water *is entering* (this depending upon the internal conditions of the plant as well as upon the soil), but the *maximum possible* rate at which it may enter if the prerequisite internal conditions arise. In this respect, then, that soil is best suited to continued physiological activity, which possesses the highest power

of supplying moisture to the absorbing regions of the plant.

It would seem, *a priori,* that a flooded soil should offer the least possible resistance to water movement, but such a soil appears indirectly to reduce water entrance in many forms by influencing (probably directly or indirectly in a chemical way) the internal conditions of the plant, and it is only with a soil in a considerably drier condition than the flooded one, that we find the optimum subterranean environment for ordinary plant processes. As the soil becomes drier, its direct resistance to water intake by the roots increases, slowly at first, then rapidly, and at a certain stage (for any given complex of aerial conditions, and hence for any given transpiration rate) the combined resultant of the movement of soil moisture to the root surfaces and that of these surfaces through the soil (by growth) falls to a magnitude so low that the processes of transpiration and of growth, etc., remove water from the tissues more rapidly than it enters below. This condition of the substratum is approximately what is usually termed the wilting point, and the remaining water in the soil is said to be unavailable for plants.

In researches which have yet to be published, my associates and I have shown that this wilting point is not the constant which it has been supposed to be, for either soil or plant. It is possible to cause the lower limit of "available" water in the soil to assume almost any magnitude, within a broad range, for any given plant, merely by altering the rate of transpiration,—through proper changes in the evaporating power of the air and the intensity of the impinging solar radiation. The wilting point thus ceases to have any meaning at all, unless the corresponding rate of transpiration is known, or unless, indeed, the aerial environment is known to be the same throughout any series of cultures the data from which are to be compared.

The primary problem, then, which must be quantitatively solved if we are to place the soil water relation in

a way that may lead to a scientific foundation, is concerned with the maximum rates at which various soils may furnish moisture to the root systems of whatever plant forms with which we may be dealing. To such an end, our knowledge of the physiology and ecology of roots must be enormously increased, but with this phase of the matter we need not here concern ourselves. It is obvious, however, that the really crucial question with regard to any soil, the properties of which we wish to study with reference to plant behavior, is this: *at what rate, and for how long a time, can it deliver water to unit area of a water-absorbing surface?* This is a purely physical question and one for which it ought not to be very difficult to find adequate methods of attack. Indeed, the method of studying evaporation from soil surfaces already offers approximate results in this direction.

This maximum rate of delivery per unit of cross section must be related in some manner to the soil characters which are now often measured; the power of water delivery will vary with the percentage of water content for any particular soil, and its graph will most likely exhibit a critical point under about the same conditions as those which accompany the critical points for evaporation from the soil, the apparent specific gravity of the latter, its penetrability (as recently brought out by Cameron and Gallagher), its critical moisture content and its moisture equivalent (as brought out by the centrifugal method of Briggs and McLane). That the critical point in maximum rate of delivery of moisture will be found to correspond to the ordinarily observed optimum water content for many plants is also to be expected, but the physiologist will not make the mistake of supposing that this optimum water content will not vary largely with the nature and condition of the plant and also with its rate of transpiration. That this critical point, with soils of varying water content, will be found to be related to the size, nature and arrangement of the soil particles is likewise fairly certain, and it may confidently be ex-

pected that this point will exhibit some definite relation to the heat of wetting (as this property has been developed by Mitscherlich), and perhaps also to the commonly determined water capacity or water-retaining power of the soil. The last named is a property which, as I have previously pointed out, seems especially worthy of investigation by ecologists who are seeking some easily determined soil characteristic for use in studies on plant distribution.

In this connection it is well to call attention to the apparent futility of the method of mechanical analysis, which is resorted to so extensively—and so expensively—in attempts physically to describe the solid portion of the soil. I think I do not exaggerate when I say that the physical analysis has shown itself to be practically worthless for any physiological purpose. It assuredly does furnish a means of describing a given soil sample with considerable accuracy, and if two samples could ever be found to exhibit exactly the same proportions of the different sized particles, it might plausibly be supposed that, *ceteris paribus,* these should possess the same relations toward water and toward plant roots, but the converse of this statement is not at all true. This method furnishes a mass of data from which no one has yet been able to derive any single comprehensive summation that will express anything definitely as to the possibilities of the given soil as a substratum for plants. Undoubtedly the size of the component soil particles plays a large part in determining how the water conductivity varies with different conditions of soil moisture, etc., but we need to seek some feature which may be much more readily measured for the soil as a whole than merely the proportions of various-sized particles.

Should we be able to find out the relations which obtain between the maximum rate of water delivery and the other soil characters that I have mentioned, it might at length become possible physically to assay a given soil by the determination of one or more of the latter, sub-

sequently passing to the real point of interest by means of an interpretation, but such a possibility is at present so far removed from actuality that it seems highly desirable to begin with attempts to measure the soil property which directly influences plants. In any event, it can not be too strongly emphasized that such soil studies as I am suggesting must always be carried on simultaneously with studies on the behavior of plants, and also with adequate determinations of the water-extracting power of the aerial environment. It seems quite likely that we shall be able empirically to determine some highly important principles bearing upon the water relations which exist between plants and soils, without having yet succeeded in analyzing the mode of manifestation of these into its elementary physical propositions—just as it has recently been possible to work out exceedingly valuable principles with reference to the relation of plants to evaporation, without any one's having yet succeeded in determining the quantitative dependence of this climatic factor upon its components, water and air temperature, air humidity and air movement.

When a little headway has been gained in the dynamic study of the soil in relation to plant processes, we shall probably begin to be able to interpret and correct, and place upon a proper quantitative basis, some of the ecological classifications of plants and the physical classifications of soils, which already occupy so much of our literature.

Another aspect of this whole question of the water relations of the subterranean parts of the terrestrial plant may be worthy of attention. The majority of the physical soil studies which have so far been made depend upon the removal of the soil sample from its natural position, with consequent and usually profound alterations in the arrangement of its component grains, upon which arrangement assuredly depend some of the most fundamental of the soil qualities which we need to know about. Various methods have been devised aiming to

avoid this difficulty, but all are exceedingly cumbersome in the operation and are at best of somewhat doubtful efficiency. Here is suggested a line of work which has already been attempted by a number of enthusiastic students, many of whom have afterward given up in despair without even publishing their experience. The director of one of the great European experiment stations told me of a somewhat elaborate apparatus which he once constructed for determining soil moisture *in situ*. He concluded with the remark, "the principle was correct enough, but the method proved useless." I am sure that he is not alone in his experience. But the problem of soil instrumentation will not be dropped; I am confident that the future will develop methods in soil physics which will not necessitate any alteration in the soil at the time a determination is made. Studies upon the soil properties in the light of their rôle in plant environment and accompanying studies on the physics of plant activities will do much toward furthering our science in this direction. The actual accomplishment of this end may not be very far off; we may take heart from such facts as this, that a single decade has sufficed to bring aerial navigation from the limbo of scoffed-at impossibility (in the minds of all but a very few scientists) into the category of accomplished fact. And the importance of adequate methods for the study of problems of the soil is far greater, and probably will ever remain far greater, than that of any problem of transportation.

To summarize my suggestions:

1. The soil water relation is of fundamental importance if we are some time to know about and be able to predict and control plant processes.

2. The moisture of the soil, as well as its other features, is most profitably to be studied as plant environment, the *relations* which obtain between plant activity and soil phenomena comprising a fundamental and primary requirement for the scientific advance of our knowledge.

3. The physical nature of the subterranean environment of terrestrial plants is effective in controlling plant activities, mainly with regard to the possible rate of delivery of water by the soil to unit area of absorbing roots.

4. It is highly desirable to study this power of water delivery with reference not only to the growth of plants but also to other soil characteristics, some of which are already commonly measured.

5. The whole problem of the physics of the subterranean surroundings of rooted plants awaits the development of an instrumentation which will not necessitate the preliminary destruction of some of the most important soil properties before the soil can really be studied.

SHORTER ARTICLES AND DISCUSSION

FURTHER NOTES REGARDING SELECTION INDEX NUMBERS[1]

THE purpose of the present communication is to correct and extend a former paper from this laboratory[2] dealing with the use of index numbers in mass selection operations. In the correspondence which the writer has had with various workers regarding that paper it would appear that a point which it was intended should be emphasized has been rather overlooked. This is that the examples of index numbers therein given for sweet corn and for poultry were intended merely to *illustrate the principles involved.* They were not put forward as the best formulæ which could be devised, even for the organisms discussed. It was pointed out that the particular formula to be used should be devised by each worker to fit his particular needs. Apparently a number of workers have adopted without change the formulæ given in our first paper. I wish again to emphasize that unless these happen to meet exactly the particular needs of the breeder, it is highly desirable that he develop formulæ of his own, involving the same general principle, but adapted to his special conditions.

I. CORRECTION OF AN ERROR IN THE FORMULA OF A SELECTION INDEX NUMBER FOR CORN

In our first paper there is an error in one of the equations for the selection index for sweet corn (*loc. cit.*, pp. 397–399).

This error has given trouble to some workers desiring to use this index number in breeding work with corn, and may cause confusion in the future. Doubtless some of those who have used the index in their work have, like the writer, made for themselves the somewhat obvious correction. Nevertheless, to insure that there may be no further confusion it seems desirable to publish a formal correction.

[1] Papers from the Biological Laboratory of the Maine Experiment Station, No. 35.

[2] Pearl, R., and Surface, F. M., "Selection Index Numbers and Their Use in Breeding." AMERICAN NATURALIST, Vol. XLIII, pp. 385–400, 1909.

The corn index number has the following formula

$$I_1 = \frac{A + 3B + 2C}{D + E + F^2}.$$

The definition of the variable C given on p. 393, by an unfortunate slip of the pen, which escaped detection in the proof, as such things will, gives precisely the inverse effect from what it should. The equation *should* read as follows:

$$C = 100 - \frac{\text{100 times the circumference of the cob at middle}}{\text{Circumference of ear at middle}}.$$

The example on p. 399, which was worked out after the text was written, followed the erroneous text with scrupulous exactitude in theory, but with a slip in the arithmetic. The correct value of I_1 for the ear used as an example is

$$I_1 = \frac{190.0 + 70.5 + 77.6}{21.6 + 2.8 + 0} = \frac{338.1}{24.4} = 13.9.$$

Experience in the use of this index suggests that in the equation for C given above it may be advantageous to substitute "diameter" for "circumference" in each case. The diameters can be much more easily and accurately measured and they probably give a better appreciation of the relative kernel depth than do the circumferences.

II. A Selection Index Number for Beans

The writer has under way at the present time some breeding experiments with a very interesting variety of beans, known locally as the "Old-fashioned Yellow Eye." It is a variety apparently scarcely known now outside of northern New England. Owing to certain defects it has been replaced in most of the bean-growing sections of the country where formerly grown by the Improved Yellow Eye, a perfectly distinct and in many respects inferior type. From the standpoint of experimental genetics the old-fashioned yellow eye bean promises to furnish material of great interest and value in the unraveling of such problems as pattern inheritance, the effect of selection in pure lines, etc.

Aside from the technically biological considerations, however,

this bean possesses much economic significance in Maine. It is esteemed above all other sorts for baking purposes, and if a strain could be developed which would possess (a) high yielding qualities, (b) reasonable disease resistance and (c) earliness and uniformity of maturing it would be of great value to the bean growers of the state. In connection with the purely biological studies an attempt is being made to see whether a pure line possessing these desirable qualities may not be found.

In this specific breeding problem we obviously have the conditions which demand the aid of selection index numbers. Several characters (not *one* only) must be concurrently selected. An estimate must be formed in each case of the *net* worth of an individual plant (or of a biotype), taking into account at least all of the three factors named. In order to do this impartially and accurately a selection index number has been devised.

In deriving this bean selection index a general equation of a slightly different type than that discussed in our former paper has been employed. In that paper (*loc. cit.*, p. 389) the general formula suggested is

$$I_1 = \frac{ax \pm by \pm cz \pm \cdots \pm uv}{a'p \pm b'q \pm c'r \pm \cdots \pm n't}.$$

In the case of beans (and very likely this may prove true for other plants and animals as well) it has seemed desirable to form an index number on the plan of the following type of equation:

$$I = \frac{axy \pm bwz \pm \cdots \pm nuv}{a'pq \pm b'rs \pm \cdots \pm n't}.$$

In this equation, as before, $a, b, c, \ldots n$, and $a', b', c' \ldots n'$ are constants, given arbitrary values in accordance with the scheme of weighing adopted, and x, y, z, w, u, v, are variables which measure characters increasing in desirability (from the breeders' standpoint) as their absolute magnitudes increase, while p, q, r, s and t are variables measuring characters which decrease in desirability as their absolute magnitudes increase. The variables specifically taken account of in the bean selection work are:

Y = Absolute yield. The weight in grams of dried shelled beans per plant.

V = Relative yield. The percentage which Y is of the weight in grams of the whole plant. This factor measures the degree to which the plant transforms its food materials into seeds rather than into foliage parts.

P = Number of pods per plant.

B = Mean number of beans per pod.

D = Disease-maturity index. The percentage which the number of perfectly matured beans free of disease (anthracnose) is of the total number of beans originally set in the pods. This measures the degree to which the *performance* of the plant in seed production approaches its *promise* in that regard. It does not separate disease resistance from earliness and completeness of maturity, but from a purely practical standpoint this is not essential. By making separate counts of diseased and immature beans it would be possible to take account of each of these factors by itself. It must be understood further that the separation of diseased beans is not absolutely complete. Only those are counted as diseased which show to the unaided eye evidence of anthracnose infection. It has not been found feasible as yet to get a simple and satisfactory measure of the degree of attack of other bean diseases. Hence, for the present, only anthracnose is being taken account of *specifically* in the selection index number.

These variables are combined in the following bean selection index number:

$$I = \frac{YP + BV}{5(100 - D)}.$$

The values taken by this index number for a particular strain of Old-fashioned Yellow Eyes are shown in Table I.

From the table it is clear that the index may take a rather wide range of values, depending upon the character of the plant. Further, the value of the index is obviously not unduly influenced by any particular variable. The high index values seem clearly to indicate the plants which are the best, *taking all things into account*. This, of course, is the goal sought.

It is of interest to note the values taken by the index in the case of a bean of quite different type, namely, a white field

TABLE I

VALUES OF THE SELECTION INDEX NUMBER FOR A SERIES OF PLANTS OF MORSE'S OLD-FASHIONED YELLOW EYE BEAN, TOGETHER WITH THE VARIABLES ON WHICH THE INDEX DEPENDS

Plant No.	Selection Index	Absolute Yield	Yield Index	Mean No. Beans per Pod	Mean Bean Weight	Total No. of Pods	Disease-Maturity Index
87[3]	.60	5.5 gms.	45.83	2.00	.55 gms.	5	60.00
85	.79	12	36.36	3.90	.47	10	33.33
86	1.24	10	41.67	3.43	.50	7	62.50
61	1.31	15	50.00	3.77	.39	13	41.45
98	1.37	7.5	41.67	3.20	.58	5	75.00
95	1.51	11	56.40	2.73	.33	15	57.77
59	1.56	13	54.17	3.78	.55	9	58.82
76	1.73	12	46.15	3.42	.43	12	54.03
62	2.00	16.1	49.53	4.33	.50	9	64.10
84	2.08	13	50.97	3.58	.43	12	67.44
71	2.58	24.5	57.64	3.47	.56	15	55.98
80	2.92	18	59.99	2.87	.49	15	69.77
89	3.26	20.5	52.58	3.71	.50	14	70.37
55	3.43	19	59.38	3.69	.42	16	69.49
69	3.73	21	59.99	3.73	.57	11	75.61
92	3.73	12	59.99	3.57	.57	7	84.00
90	3.83	19.5	59.10	3.33	.53	12	77.50
56	3.97	30.9	59.42	4.33	.47	18	58.97
63	4.17	23	51.10	4.53	.41	17	70.13
75	5.35	39	59.99	4.07	.47	27	55.86
81	5.51	27	64.27	3.18	.51	17	75.93
68	7.32	27	59.99	3.42	.46	19	80.38
70	7.37	26	61.16	3.59	.46	17	82.06
60	7.56	19	55.07	3.38	.36	16	87.04
78	8.47	29	61.70	3.19	.46	21	80.97
66	8.79	30	63.17	4.14	.56	14	84.48
67	9.42	23	52.88	3.68	.34	19	86.59
83	9.50	26	59.10	3.14	.43	22	84.06
82	10.09	30	61.24	3.67	.46	18	98.48
97	10.38	50.5	44.11	5.42	.29	41	57.21
79	15.30	30	62.50	3.48	.43	21	88.93
73	17.04	38	60.31	3.89	.42	26	86.14

pea bean. Table II gives the index and component variables for a series of plants of such a variety.

The range of values here is large. The extremely high values are probably much larger than will ever be obtained for a bean of the yellow eye type, though it is rather risky to make such a prophecy. Two factors help in reaching such high index values in the case of this variety. One is the tendency to prolificacy, there being relatively many pods per plant and beans per pod. The other is the rather high disease resistance of the

[3] Plant injured by cut worms.

[4] Plant injured by cut worms, but subsequently grew.

plants. They mature, apparently free from disease, a large proportion of their seeds.

TABLE II

VALUES OF THE SELECTION INDEX NUMBERS FOR A SERIES OF PLANTS OF SNOW FLAKE FIELD BEANS

Plant No.	Selection Index	Absolute Yield	Yield Index	Mean No. Beans per Pod	Mean Bean Weight	Total No. per Pod	Disease-Maturity Index
186[4]	3.09	7	31.82	4.13	.21	8	87.88
192[4]	4.42	23	46.95	5.30	.16	33	54.42
187	6.31	6.5	44.82	5.86	.17	7	90.24
191	12.25	38	56.72	6.06	.24	34	73.30
183	12.86	9	54.56	4.10	.22	10	95.12
190	25.44	55	48.24	5.10	.30	42	79.91
188	30.72	60	47.80	5.35	.32	40	82.71
184	71.98	50.5	57.14	5.64	.19	52	91.81
185	101.12	40	57.14	5.35	.22	34	96.71

Of course, the index numbers may, strictly speaking, be compared only among plants of the same variety. The absolute desirability of a variety for a particular purpose depends upon many other factors not taken account of in the index number. These numbers can not be used directly and solely as measures of the relative worth of varieties.

It is hoped that this bean selection index number or some modification of it may be found useful by other workers. It will, at any rate, serve to illustrate further the adaptability of the general idea of such numbers to a wide range of practical selection work. In the present instance a selection index number is applied to the measurement of the relative worth of different distinct biotypes, rather than in the mass selection of fluctuating variations, in which latter type of work such numbers were shown in our former communication to be useful.

RAYMOND PEARL

UNIVERSITY OF MAINE

NOTES AND LITERATURE

PROTOZOA[1]

THAT so expensive and highly specialized a text-book as this of Doflein's should run through a whole edition in less than a year is a tribute to the excellence of the work and an index to the scientific activity in this field of biological research. An indication of the rapid progress now in the making in protozoology may be derived from the fact that every chapter in this elaborate work has been rewritten or substantially emended and the number of pages and illustrations increased by fifteen per cent. in this third edition, the second having been issued less than two years ago. The main changes include the insertion of a chapter on the origin of the Protozoa, the conception of species within the group, and the phenomena of variation and heredity as revealed by methods of culture and experiment, especially by the study of pure lines and the results of selection. Doflein calls attention to the appearance of direct adaptations in parasitic organisms in response to definite environmental factors in the form of chemical substances such as atoxyl and various compounds of arsenic and of antimony, unknown in the normal environment of the protozoan organism. These adaptations result in so-called resistant races and may be heritable. The possibility of control, the large numbers available and the rapidity of multiplication of these pathogenic organisms unite to open an inviting field, thus far too much neglected by the investigator in experimental evolution.

Considerable additions are made to the discussion of reproduction, especially to the maturation of the gametes, in which homologies to maturation in the Metazoa are becoming increasingly definite. The detailed discussion of the various groups of protozoa is noticeably extended in the case of the Spirochætes, the Hæmosporidia and the Sarcosporidia.

[1] "Lehrbuch der Protozoenkunde. Eine Darstellung der Naturgeschichte der Protozoen mit besonderer Berücksichtigung der parasitischen und pathogenen Formen." Dritte stark vermehrte Auflage. Von Dr. F. Doflein. xii + 1043 pp., mit 951 Abbildungen im Text. Jena, Gustav Fischer, 1911. M. 26, gb. M. 28.50.

Doflein is inclined to accept the evidence that Schaudinn's account of *Entamœba histolytica* is based in part upon phenomena attendant upon processes of degeneration and suggests that Viereck's *E. tetragena* is probably the most widespread form causing amœbic dysentery, and that the two are possibly identical, but that the organism according to the rigid laws of priority should be called *Entamœba dysenteriæ* (Councilman and Lafleur).

The doubtful group Chlamydozoa established by Prowazek for that group of immunizing organisms with a filterable virus, the supposed etiological factors in such diseases as vaccinia, variola, trachoma, molluscum contagiosum and epithelioma contagiosum, is still denied admittance by the author to the Protozoa on the ground that the minute structures described by Prowazek are not themselves with certainty proved to be living organisms. Doflein admits, however, that the evidence is constantly increasing that we have to do in the case of these diseases with parasitic organisms, but thinks they may be more closely related to the bacteria than to the protozoa.

It is a matter of regret that the non-parasitic groups, such, for example, as the pelagic Foraminifera and Radiolaria, and non-parasitic flagellates can not receive in a work of this sort commensurate treatment with pathogenic forms of confessedly great biological, as well as medical and hygienic interest. The author expresses the hope that medical research may in the near future so clear up contested points that less space will be required for the discussion of pathogenic forms. The present output is, however, not very promising for a reduction in extent in this field. The fact is that a six-volume edition of the Protozoa in Bronn's "Thiereich" is needed to give anything like an adequate review of the results now achieved in the fields of Protozoology.

Charles Atwood Kofoid

University of California

HEREDITY

H. M. Leake[14] gives additional results of his studies of inheritance in cotton. The flower color factors found were yellow, pale yellow and red, the latter being due to red sap color which showed not only in the flowers but in stems and leaves as well.

[14] "Studies in Indian Cotton," *Jour. of Gen.*, Aug., 1911.

Yellow was completely dominant to its absence and to pale yellow. Red was incompletely dominant. The very interesting fact developed that although yellow behaved as an allelomorph to its absence in crosses with white, it was also allelomorphic to pale yellow in crosses with the latter. This indicates that pale yellow is simply a modified form of yellow, a fact in entire accord with my teleone theory of Mendelian inheritance, and opposed to the de Vriesian idea of the immutability of the so-called unit characters. An interesting case of correlation was found. White (absence of yellow) is hardier than yellow.

In shape of leaf Leake uses as an empirical means of describing leaf shape a formula which is essentially the ratio between the length and breadth of the central lobe. The pure races (and the author took the pains to work with pure races) may be divided into two groups with reference to this "leaf factor," namely those in which it is less than 2, and those in which it is greater than 3. No cases were found in pure races in which the value of this factor was between 2 and 3. F_1 between these groups gave intermediate leaf factors. F_2 apparently behaved as if the cross involved a single gene, but fluctuating variation obscured the results considerably. Crosses between F_1 and either parent form gave only the intermediate and the one parent form, the same difficulty appearing from fluctuation in the character. This strongly confirms the conclusion that a single gene is responsible for the difference between these two groups.

Earliness of flowering $\times$ late flowering proved to be a very interesting study. The author had previously discovered that types with sympodial secondary branches flower early, while those having monopodial secondaries are late flowering. This relation had also been noticed by others, the early or late flowering being a result of the manner of branching. Length of vegetative period (time between planting and first flower) proved to be highly fluctuating, varying widely as between different seasons. F_1 between the monopodial and the sympodial types was intermediate between the parents, but nearer the sympodial (early) parent. F_2 gave a continuous series extending from the early parent nearly to the late parent, the frequency curve for the earliness in the F_2 population being monomodal. While the author does not pursue the subject further, it may easily be shown that this is exactly what Mendelian theory calls for on the assumption that several factors, each alike in effect, their

effects being additive, are responsible for the parental differences, especially when the character in question fluctuates widely as compared with the differences between the several genotypes occurring in F_2. Thus, suppose three factors, *A, B* and *C,* each alike in effect, and each producing the same average increase in length of vegetative period. The F_2 generation of the cross *abc* × *ABC* will consist of the genotypes *aabbcc, aabbCC, aaBBcc, AAbbcc, aaBBCC, AAbbCC, AABBcc* and *AABBCC* and their crosses. The genotype *aabbcc* would be similar to the early parent. Genotypes *AAbbcc, aaBBcc* and *aabbCC* would constitute a group one stage later in flowering. *AABBcc, AAbbCC* and *aaBBCC* constitute a third stage, while *AABBCC* would be equivalent to the late parent. Thus the four stages resulting from these three factors tend to be present in the ratio 1 : 3 : 3 : 1, which ratio is merely one way of stating the properties of an ordinary frequency curve. Earliness being nearly completely dominant, the norm of this curve would be shifted toward the early parent, as Leake found was the case. Even if this progeny were selfed to the tenth generation, by which time heterozygosis would have largely disappeared, the mixture of the four genotypes would still give a monomodal curve. The only exception to this would be cases in which fluctuating variation is not transgressive between the genotypes. It is possible that more than three genes were involved in Leake's crosses.

Crosses between pure lines having no leaf glands and those having leaf glands gave intermediate F_1. F_2 gave evidence of segregation, but the intermediate and apparently highly fluctuating character of the heterozygotes rendered positive conclusions difficult or impracticable.

Complete correlation occurred between flower color and length of petals. White petals were little if any longer than the bracteoles, while yellow petals were about twice as long. Intermediates did not occur, and no exceptions were found in over 100,000 plants.

Red sap color was independent of the size of the petal but when present it lengthened the vegetative period. This paper is exceedingly clear and lucid in treatment, and we may expect much valuable work from the author in future.

Dr. Shull has resumed his interesting studies of *Bursa.*[15] He

[15] Dr. G. H. Shull, "Defective Inheritance-Ratios in *Bursa* Hybrids," *Verh. d. Naturforsch.* Ver. in Brünn., Bd. XLIX.

had previously shown that four genotypes of *Bursa bursa-pastoris* are the four Mendelian types corresponding to two independent factors (*AABB*, *AAbb*, *aaBB*, *aabb*). In his paper above cited he deals with a cross between one of these types (*aabb*) with a genotype of *Bursa Heegeri* corresponding to the type *AABB*. The factors *A* and *B* in this cross behave in the usual Mendelian fashion, departures from expected ratios being explained by variation in dominance in one of the families. But the factor or factors governing differences in the seed pod of these two species present departures from expected ratios that are not fully understood. There is evidence that at least two genes are concerned in this difference. If only one gene were concerned the ratio between the two types of seed capsule in F_2 should be 3:1; if there are two genes, the ratio should be 15:1, three genes, 63:1. The ratios observed in F_3 were 4.67:1 (instead of 3:1), 15.6:1, 24:1 and 63.5:1. The latter ratio, obtained in a rather large family (129 individuals), suggests three genes. The first and fourth of the above ratios are rather wide departures from expected ratios, and their meaning is not yet clear. The matter is still under investigation. There seems to be little doubt that Dr. Shull has added another case to the interesting class of Mendelian characters that may be represented by more than one independent gene, such as those found by Nillson-Ehle, in oats and wheat and by East in corn.

A very interesting paper by Gortner,[16] giving further results of his studies on melanin formation, appeared in the December (1911) number of this journal. He was able to show the color pattern in the Colorado potato beetle is due to the fact that the chromogen is secreted only in certain spots, while the oxidizing enzyme, which is of the tyrosinase type, is present generally in the elytron.

W. J. SPILLMAN

[16] Dr. R. A. Gortner, "Studies on Melanin," AMER. NAT., Vol. XLV, No. 540, pp. 743 et seq.